CHAPTER 15
PLANT GROWTH AND DEVELOPMENT

- Trees continue to increase in height or girth over a period of time.
- However, the leaves, flowers and fruits of the same tree not only have limited dimensions but also appear and fall periodically and sometime repeatedly.
- Development is the sum of two processes: growth and differentiation.

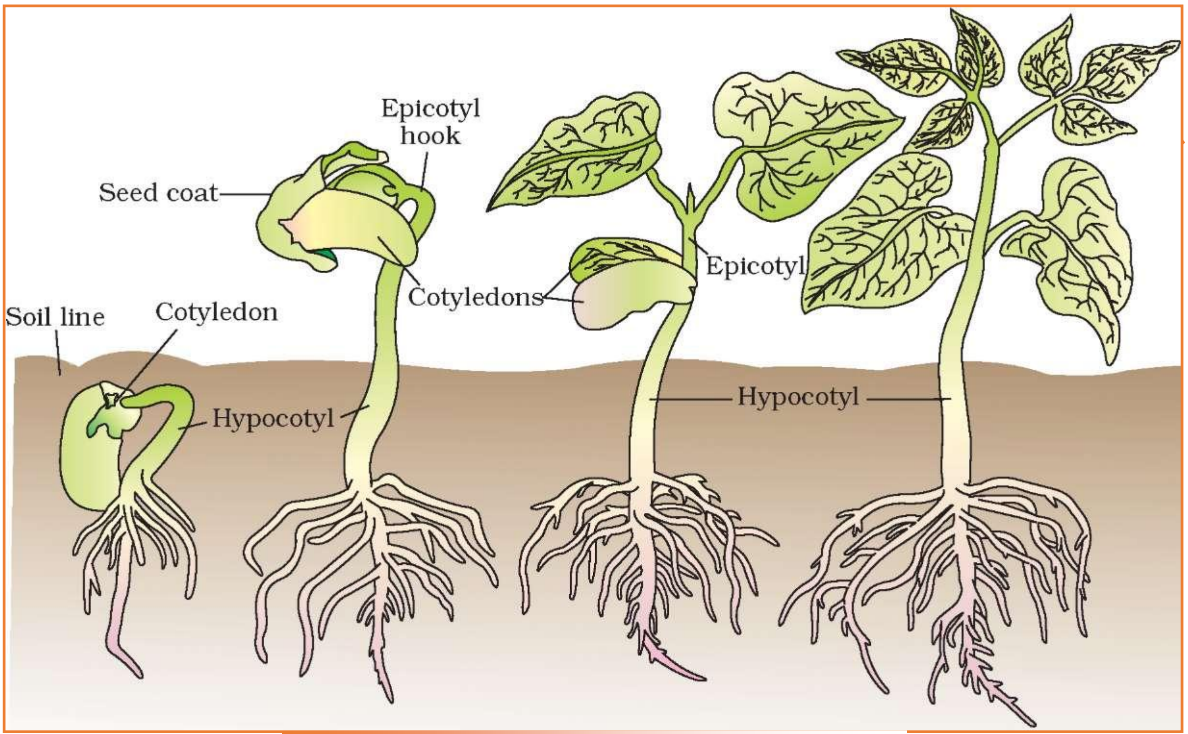

Fig: Germination and seedling development in bean

GROWTH

- Growth is regarded as one of the most fundamental and conspicuous characteristics of a living being.
- Growth can be defined as an irreversible permanent increase in size of an organ or its parts or even of an individual cell.
- Generally, growth is accompanied by metabolic processes (both anabolic and catabolic), that occur at the expense of energy. Therefore, expansion of a leaf is growth while swelling of piece of wood when placed in water is not.

Plant Growth Generally is Indeterminate

- Plant growth is unique because plants retain the capacity for unlimited growth throughout their life.
- This ability of the plants is due to the presence of meristems at certain locations in their body.
- The cells of such meristems have the capacity to divide and self-perpetuate.
- The product, however, soon loses the capacity to divide and such cells make up the plant body.

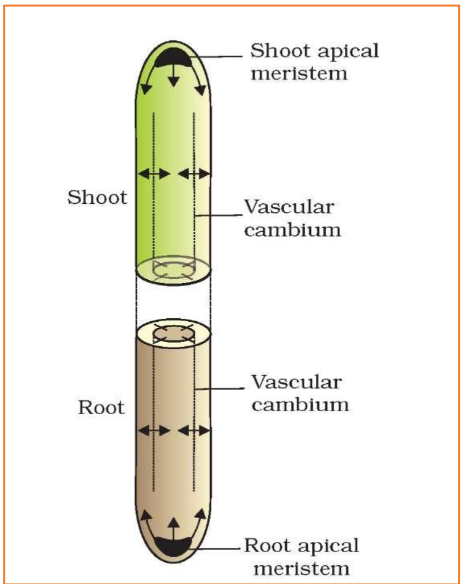

Fig: Diagrammatic representation of locations of root apical meristem, shoot aplical meristem and vascular cambium. Arrows exhibit the direction of growth of cells and organ.

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- This form of growth wherein new cells are always being added to the plant body by the activity of the meristem is called the open form of growth.
- The root apical meristem and the shoot apical meristem are responsible for the primary growth of the plants and principally contribute to the elongation of the plants along their axis.
- In dicotyledonous plants and gymnosperms, the lateral meristems, vascular cambium and cork-cambium appear later in life and cause the increase in the girth of the organs in which they are active. This is known as secondary growth of the plant.

Growth is Measurable

- Growth, at a cellular level, is principally a consequence of increase in the amount of protoplasm. Since increase in protoplasm is difficult to measure directly, one generally measures some quantity which is more or less proportional to it.
- Growth is, therefore, measured by a variety of parameters some of which are: increase in fresh weight, dry weight, length, area, volume and cell number.

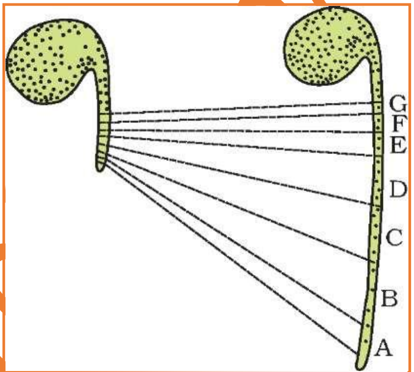

Fig: Detection of zones of elongation by the parallel line technique. Zones A, B, C, D immediately behind the apex have elongated most.

Phases of Growth

- The period of growth is generally divided into three phases, namely, meristematic, elongation and maturation.
- The constantly dividing cells, both at the root apex and the shoot apex, represent the meristematic phase of growth. The cells in this region are rich in protoplasm, possess large conspicuous nuclei. Their cell walls are primary in nature, thin and cellulosic with abundant plasmodesmatal connections.
- The cells proximal (just next, away from the tip) to the meristematic zone represent the phase of elongation. Increased vacuolation, cell enlargement and new cell wall deposition are the characteristics of the cells in this phase.
- Further away from the apex, i.e., more proximal to the phase of elongation, lies the portion of axis which is undergoing the phase of maturation. The cells of this zone, attain their maximal size in terms of wall thickening and protoplasmic modifications.

Growth Rates

- The increased growth per unit time is termed as growth rate.
- Thus, rate of growth can be expressed mathematically.
- The growth rate shows an increase that may be arithmetic or geometrical.
- In arithmetic growth, following mitotic cell division, only one daughter cell continues to divide while the other differentiates and matures. The simplest expression of arithmetic growth is exemplified by a root elongating at a constant rate.
  On plotting the length of the organ against time, a linear curve is obtained. Mathematically, it is expressed as $L_t = L_o + rt$
  L_t = length at time 't'
  L_0 = length at time 'zero'
  r = growth rate / elongation per unit time.
- In geometrical growth, the initial growth is slow (lag phase), and it increases rapidly thereafter - at an exponential rate (log or exponential phase). Here, both the progeny cells following mitotic cell division retain the ability to divide and continue to do so. However, with limited nutrient supply, the growth slows down leading to a stationary phase.
- If we plot the parameter of growth against time, we get a typical sigmoid or S-curve. A sigmoid curve is a characteristic of living organism growing in a natural environment. It is typical for all cells, tissues and organs of a plant.
- The exponential growth can be expressed as

$W_t = W_0 e^{rt}$
W_t = final size (weight, height, number etc.)
W_0 = initial size at the beginning of the period
r = growth rate
t = time of growth
e = base of natural logarithms.
Here, r is the relative growth rate and is also the measure of the ability of the plant to produce new plant material, referred to as efficiency index. Hence, the final size of W_1 depends on the initial size, W_0.

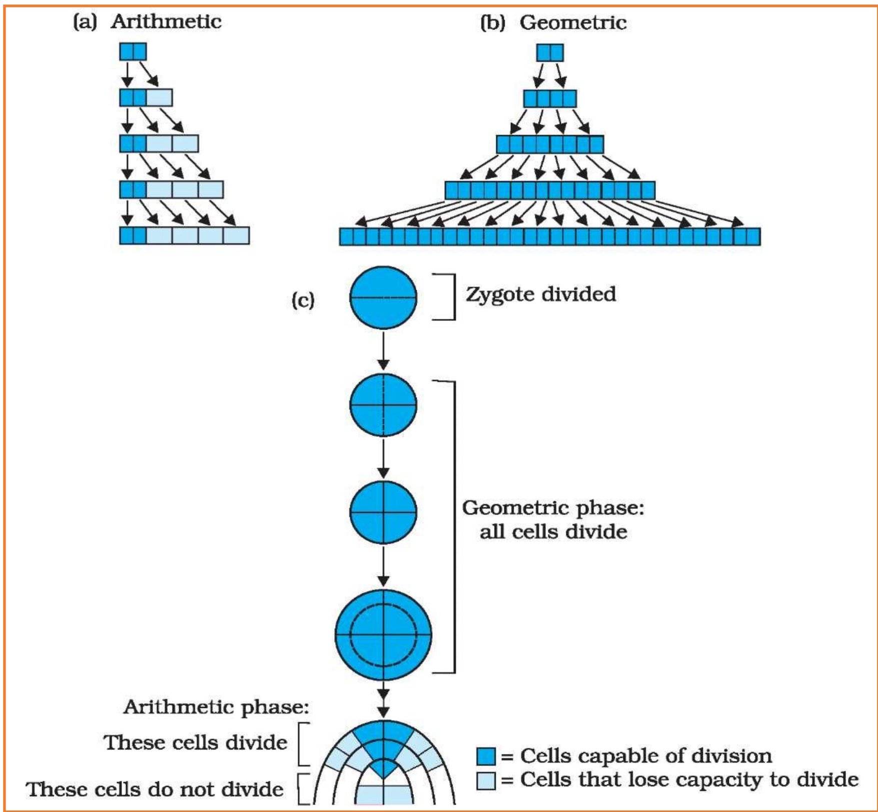

Fig: Diagrammatic representation of: (a) Arithmetic (b) Geometric growth and (c) Stages during embryo development showing geometric and arithmetic phases

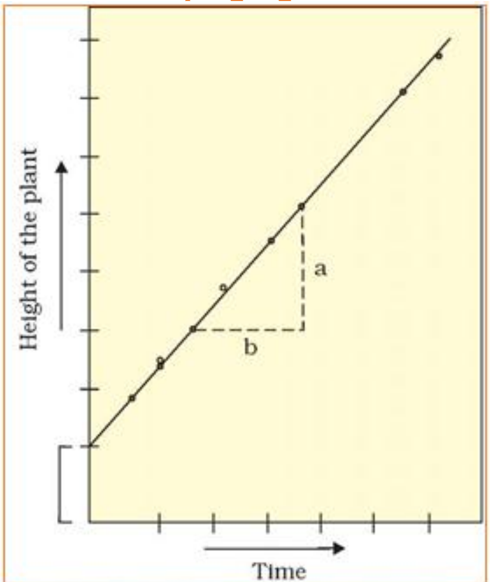

Fig: Constant linear growth, a plot of length L against time t

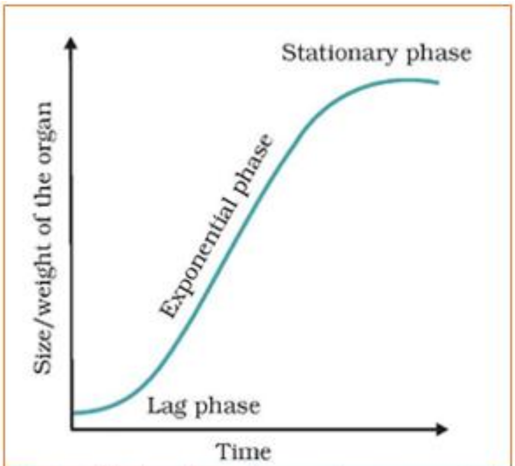

Fig: An idealised sigmoid growth curve typical of cells in culture, and many higher plants and plant organs.

- Quantitative comparisons between the growth of living system can also be made in two ways :
  (i) measurement and the comparison of total growth per unit time is called the absolute growth rate.
  (ii) The growth of the given system per unit time expressed on a common basis, e.g., per unit initial parameter is called the relative growth rate.

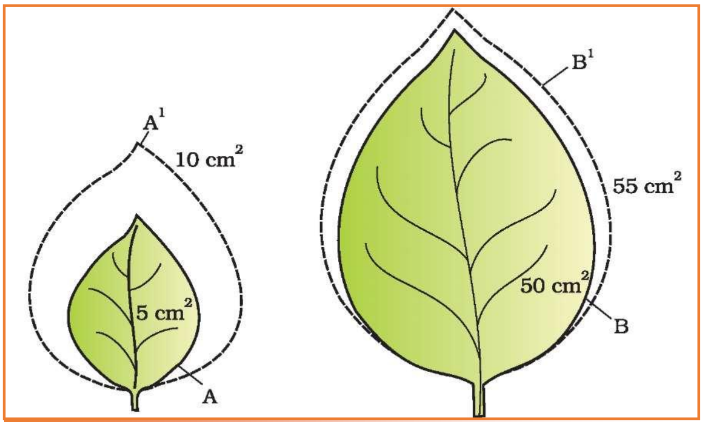

Fig: Diagrammatic comparison of absolute and relative growth rates. Both leaves A and B have increased their area by 5 cm^2 in a given time to produce A^1, B^1 leaves.

Conditions for Growth

- water, oxygen and nutrients are very essential elements for growth.
- The plant cells grow in size by cell enlargement which in turn requires water. Turgidity of cells helps in extension growth. Thus, plant growth and further development is intimately linked to the water status of the plant. Water also provides the medium for enzymatic activities needed for growth.
- oxygen helps in releasing metabolic energy essential for growth activities.
- Nutrients (macro and micro essential elements) are required by plants for the synthesis of protoplasm and act as source of energy.
- In addition, every plant organism has an optimum temperature range best suited for its growth. Any deviation from this range could be detrimental to its survival.
- Environmental signals such as light and gravity also affect certain phases/stages of growth.

Differentiation, Dedifferentiation and Redifferentiation

- The cells derived from root apical and shoot-apical meristems and cambium differentiate and mature to perform specific functions. This act leading to maturation is termed as **differentiation.**
- During differentiation, cells undergo few to major structural changes both in their cell walls and protoplasm. For example, to form a tracheary element, the cells would lose their protoplasm. They also develops a very strong, elastic, lignocellulosic secondary cell walls, to carry water to long distances even under extreme tension.
- differentiated cells, that have lost the capacity to divide can regain the capacity of division under certain conditions. This phenomenon is termed as **dedifferentiation.** For example, formation of meristems - interfascicular cambium and cork cambium from fully differentiated parenchyma cells.
  While doing so, such meristems/tissues are able to divide and produce cells that once again lose the capacity to divide but mature to perform specific functions, i.e., get **redifferentiated.**
- Growth in plants is open, i.e., it can be indeterminate or determinate. Now, we may say that even differentiation in plants is open, because cells/tissues arising out of the same meristem have different structures at maturity.
- The final structure at maturity of a cell/tissue is also determined by the location of the cell within. For example, cells positioned away from root apical meristems differentiate as root-cap cells, while those pushed to the periphery mature as epidermis.

DEVELOPMENT

- Development is a term that includes all changes that an organism goes through during its life cycle from germination of the seed to senescence.

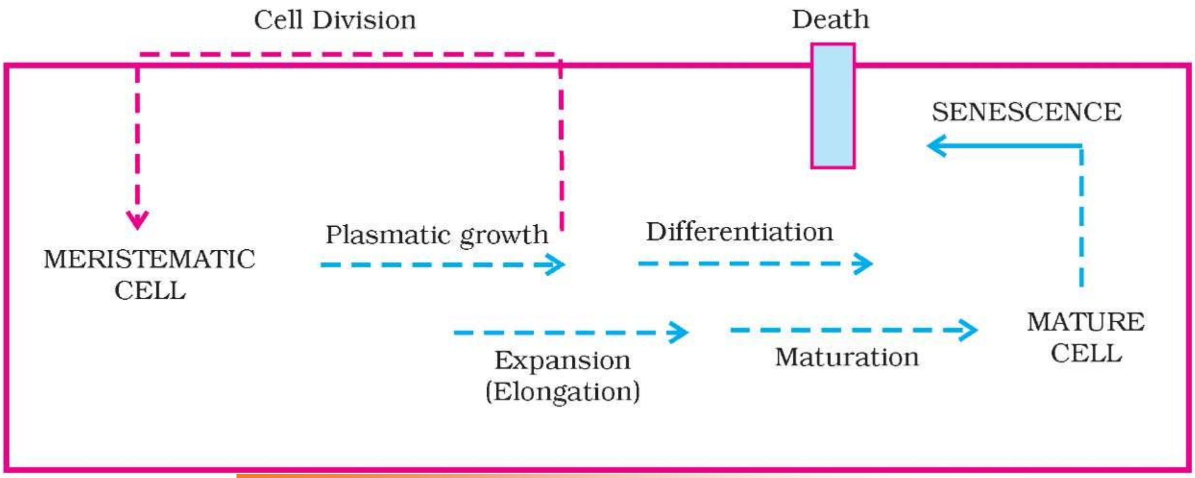

Fig: Sequence of the developmental process in a plant cell

- Plants follow different pathways in response to environment or phases of life to form different kinds of structures. This ability is called **plasticity,** e.g., heterophylly in cotton, coriander and larkspur.
  In such plants, the leaves of the juvenile plant are different in shape from those in mature plants.
- On the other hand, difference in shapes of leaves produced in air and those produced in water in buttercup also represent the heterophyllous development due to environment. This phenomenon of heterophylly is an example of plasticity.

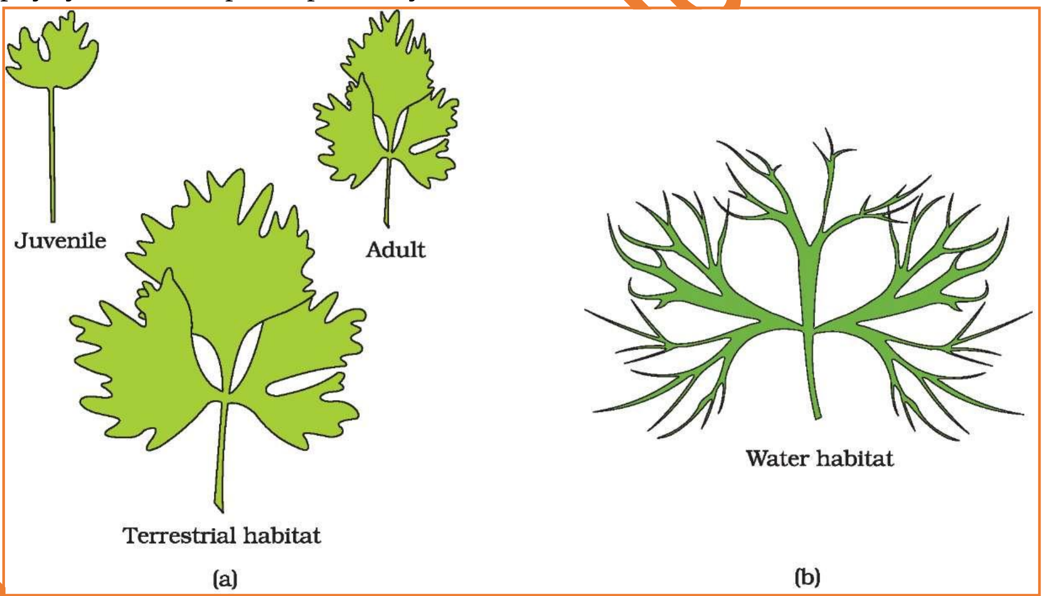

Fig: Heterophylly in (a) larkspur and (b) buttercup

- Thus, growth, differentiation and development are very closely related events in the life of a plant. Broadly, development is considered as the sum of growth and differentiation.
- Development in plants (i.e., both growth and differentiation) is under the control of intrinsic and extrinsic factors. The former includes both intracellular (genetic) or intercellular factors (chemicals such as plant growth regulators) while the latter includes light, temperature, water, oxygen, nutrition, etc.

PLANT GROWTH REGULATORS

Characteristics

- The plant growth regulators (PGRs) are small, simple molecules of diverse chemical composition.
- They could be
  - indole compounds (indole-3-acetic acid, IAA);
  - adenine derivatives (N^6-furfurylamino purine, kinetin),
  - derivatives of carotenoids (abscisic acid, ABA);
  - terpenes (gibberellic acid, GA_3) or
  - gases (ethylene, C_2H_4).
- Plant growth regulators are variously described as plant growth substances, plant hormones or phytohormones in literature.
- The PGRs can be broadly divided into two groups based on their functions in a living plant body.
- One group of PGRs are involved in growth promoting activities, such as cell division, cell enlargement, pattern formation, tropic growth, flowering, fruiting and seed formation. These are also called plant growth promoters, e.g., auxins, gibberellins and cytokinins.
- The PGRs of the other group play an important role in plant responses to wounds and stresses of biotic and abiotic origin. They are also involved in various growth inhibiting activities such as dormancy and abscission. The PGR abscisic acid belongs to this group.
- The gaseous PGR, ethylene, could fit either of the groups, but it is largely an inhibitor of growth activities.

The Discovery of Plant Growth Regulators

- Interestingly, the discovery of each of the five major groups of PGRs have been accidental.
- **Charles Darwin and his son Francis Darwin** – observed phototropism in Canary grass.
- **F.W. Went** – isolated Auxin from tips of coleoptiles of oat seedlings.
- **E. Kurosawa** – reported the appearance of symptoms of the 'Bakane disease' in uninfected rice seedlings when they were treated with sterile filtrates of the fungus *Gibberalla fujikuroi*. The active substances were later identified as gibberellic acid.
- **F. Skoog and co-workers** – observed callus proliferation in tobacco callus in presence of extracts of vascular tissues/yeast extract/coconut milk or DNA in addition to Auxins.
- **Skoog and Miller** – identified and crystallised the cytokinesis promoting active substance and termed it kinetin.
- **Cousins** – confirmed the release of a volatile substance from ripened oranges that hastened the ripening of stored unripened bananas. Later this volatile substance was identified as ethylene, a gaseous PGR
- During mid-1960s, three independent researches reported the purification and chemical characterisation of three different kinds of inhibitors: inhibitor-B, abscission II and dormin. Later all the three were proved to be chemically identical. It was named abscisic acid (ABA).

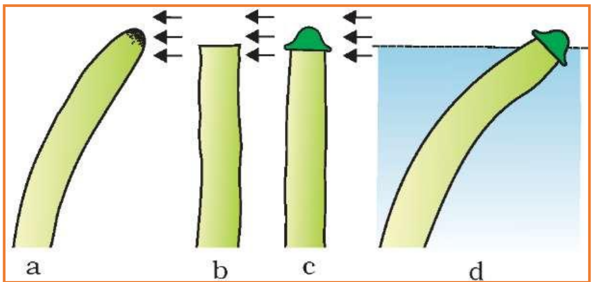

Fig: Experiment used to demonstrate that tip of the coleoptile is the source of auxin. Arrows indicate direction of light

PHYSIOLOGICAL EFFECTS OF PLANT GROWTH REGULATORS

AUXINS

- Auxins (from Greek 'auxein' : to grow) was first isolated from human urine.
- The term 'auxin' is applied to the indole-3-acetic acid (IAA), and to other natural and synthetic compounds having certain growth regulating properties.
- They are generally produced by the growing apices of the stems and roots, from where they migrate to the regions of their action.
- Auxins like IAA and indole butyric acid (IBA) have been isolated from plants.
- NAA (naphthalene acetic acid) and 2, 4-D (2, 4-dichlorophenoxyacetic) are synthetic auxins.
- All these auxins have been used extensively in agricultural and horticultural practices.
- They help to initiate rooting in stem cuttings, an application widely used for plant propagation.
- Auxins promote flowering e.g. in pineapples.
- They help to prevent fruit and leaf drop at early stages but promote the abscission of older mature leaves and fruits.
- In most higher plants, the growing apical bud inhibits the growth of the lateral (axillary) buds, a phenomenon called **apical dominance.** Removal of shoot tips (decapitation) usually results in the growth of lateral buds. It is widely applied in tea plantations, hedge-making.
- Auxins also induce parthenocarpy, e.g., in tomatoes.
- They are widely used as herbicides. 2, 4-D, widely used to kill dicotyledonous weeds, does not affect mature monocotyledonous plants.
- It is used to prepare weed-free lawns by gardeners.
- Auxin also controls xylem differentiation and helps in cell division.

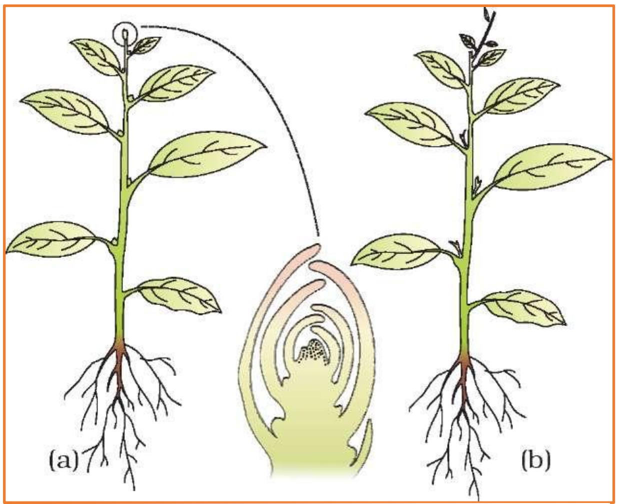

Fig: Apical dominance in plants :
(a) A plant with apical bud intact
(b) A plant with apical bud removed Note the growth of lateral buds into branches after decapitation.

GIBBERELLINS

- There are more than 100 gibberellins reported from widely different organisms such as fungi and higher plants. They are denoted as GA_1, GA_2, GA_3 and so on.
- However, Gibberellic acid (GA_3) was one of the first gibberellins to be discovered and remains the most intensively studied form.
- All GAs are acidic.
- They have ability to cause an increase in length of axis. It is used to increase the length of grapes stalks.
- Gibberellins, cause fruits like apple to elongate and improve its shape.
- They also delay senescence. Thus, the fruits can be left on the tree longer so as to extend the market period.
- GA_3 is used to speed up the malting process in brewing industry.
- Sugarcane stores carbohydrate as sugar in their stems. Spraying sugarcane crop with gibberellins increases the length of the stem, thus increasing the yield by as much as 20 tonnes per acre.
- Spraying juvenile conifers with GAs hastens the maturity period, thus leading to early seed production.

- Gibberellins also promotes bolting (internode elongation just prior to flowering) in beet, cabbages and many plants with rosette habit.

CYTOKININS

- Cytokinins have specific effects on cytokinesis, and were discovered as kinetin (a modified form of adenine, a purine) from the autoclaved herring sperm DNA.
- Kinetin does not occur naturally in plants.
- Search for natural substances with cytokinin-like activities led to the isolation of zeatin from corn-kernels and coconut milk.
- Since the discovery of zeatin, several naturally occurring cytokinins, and some synthetic compounds with cell division promoting activity, have been identified.
- Natural cytokinins are synthesised in regions where rapid cell division occurs, for example, root apices, developing shoot buds, young fruits etc.
- It helps to produce new leaves, chloroplasts in leaves, lateral shoot growth and adventitious shoot formation.
- Cytokinins help overcome the apical dominance.
- They promote nutrient mobilisation which helps in the delay of leaf senescence.

ETHYLENE

- Ethylene is a simple gaseous PGR.
- It is synthesised in large amounts by tissues undergoing senescence and ripening fruits.
- Influences of ethylene on plants include horizontal growth of seedlings, swelling of the axis and apical hook formation in dicot seedlings.
- Ethylene promotes senescence and abscission of plant organs especially of leaves and flowers.
- Ethylene is highly effective in fruit ripening.
- It enhances the respiration rate during ripening of the fruits. This rise in rate of respiration is called respiratory climactic.
- Ethylene breaks seed and bud dormancy, initiates germination in peanut seeds, sprouting of potato tubers.
- Ethylene promotes rapid internode/petiole elongation in deep water rice plants.
- It helps leaves/ upper parts of the shoot to remain above water.
- Ethylene also promotes root growth and root hair formation, thus helping the plants to increase their absorption surface.
- Ethylene is used to initiate flowering and for synchronising fruit-set in pineapples.
- It also induces flowering in mango.
- Since ethylene regulates so many physiological processes, it is one of the most widely used PGR in agriculture.
- The most widely used compound as source of ethylene is **ethephon**.
- Ethephon in an aqueous solution is readily absorbed and transported within the plant and releases ethylene slowly.
- Ethephon hastens fruit ripening in tomatoes and apples and accelerates abscission in flowers and fruits (thinning of cotton, cherry, walnut).
- It promotes female flowers in cucumbers thereby increasing the yield.

ABSCISIC ACID

- Abscisic acid **(ABA)** was discovered for its role in regulating abscission and dormancy.
- It acts as a general plant growth inhibitor and an inhibitor of plant metabolism.
- ABA inhibits seed germination.
- ABA stimulates the closure of stomata in the epidermis and increases the tolerance of plants to various kinds of stresses. Therefore, it is also called the stress hormone.

- ABA plays an important role in seed development, maturation and dormancy.
- By inducing dormancy, ABA helps seeds to withstand desiccation and other factors unfavourable for growth.
- In most situations, ABA acts as an antagonist to GAs.

- There are a number of events in the life of a plant where more than one PGR interact to affect that event, e.g., dormancy in seeds/ buds, abscission, senescence, apical dominance, etc.
- The role of PGR is of only one kind of intrinsic control. Along with genomic control and extrinsic factors, they play an important role in plant growth and development.
- Many of the extrinsic factors such as temperature and light, control plant growth and development via PGR.
- Some of such events could be: vernalisation, flowering, dormancy, seed germination, plant movements, etc.

PHOTOPERIODISM

- Some plants require a periodic exposure to light to induce flowering. Such plants are able to measure the duration of exposure to light.
- For example, some plants require the exposure to light for a period exceeding a well defined critical duration, while others must be exposed to light for a period less than this critical duration before the flowering is initiated in them. The former group of plants are called **long day plants** while the latter ones are termed **short day plants.**
- The critical duration is different for different plants.
- There are many plants, however, where there is no such correlation between exposure to light duration and induction of flowering response; such plants are called **day-neutral plants**.

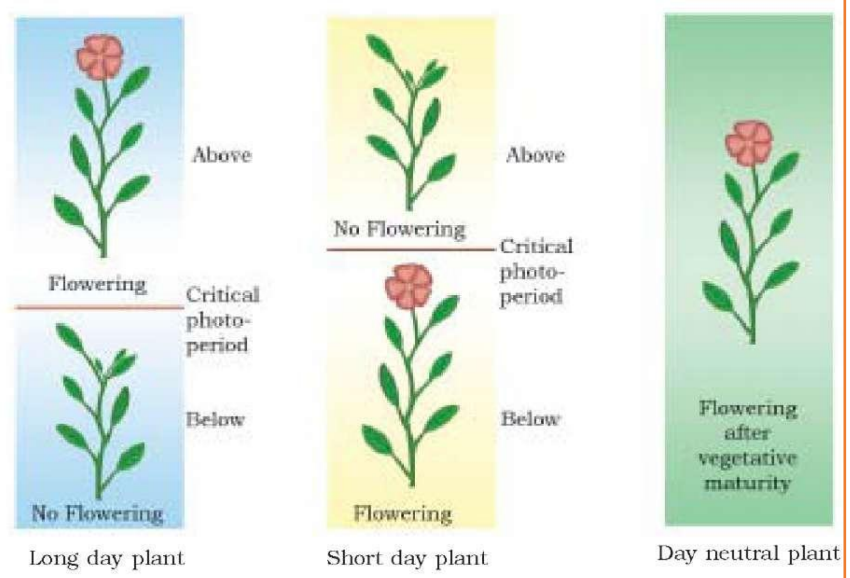

Fig: Photoperiodism : Long day, short day and day neutral plants

- It is now also known that not only the duration of light period but that the duration of dark period is also of equal importance.
- Hence, it can be said that flowering in certain plants depends not only on a combination of light and dark exposures but also their relative durations. This response of plants to periods of day/night is termed **photoperiodism.**
- It is also interesting to note that while shoot apices modify themselves into flowering apices prior to flowering, they (i.e., shoot apices of plants) by themselves cannot percieve photoperiods.
- The site of perception of light/dark duration are the leaves.
- It has been hypothesised that there is a hormonal substance(s) that is responsible for flowering.
- This hormonal substance migrates from leaves to shoot apices for inducing flowering only when the plants are exposed to the necessary inductive photoperiod.

VERNALISATION

- There are plants for which flowering is either quantitatively or qualitatively dependent on exposure to low temperature. This phenomenon is termed **vernalisation.**
- It prevents precocious reproductive development late in the growing season, and enables the plant to have sufficient time to reach maturity.
- Vernalisation refers specially to the promotion of flowering by a period of low temperature.
- Some important food plants, wheat, barley, rye have two kinds of varieties: winter and spring varieties.
- The 'spring' variety are normally planted in the spring and come to flower and produce grain before the end of the growing season.
- Winter varieties, however, if planted in spring would normally fail to flower or produce mature grain within a span of a flowering season. Hence, they are planted in autumn.
- They germinate, and over winter come out as small seedlings, resume growth in the spring, and are harvested usually around mid-summer.
- Another example of vernalisation is seen in biennial plants.
- Biennials are monocarpic plants that normally flower and die in the second season.
- Sugerbeet, cabbages, carrots are some of the common biennials.
- Subjecting the growing of a biennial plant to a cold treatment stimulates a subsequent photoperiodic flowering response.