Plant Growth and Development

CONTENTS

6. PLANT GROWTH AND DEVELOPMENT

6.1 Introduction

- Growth in living organism is intrinsic.
- Growth is the most important phenomenon of all living organisms.
- Plant Growth is an irreversible increase in size, weight and volume of an organism or its parts.
- Growth in plants occurs by cell division, cell elongation and cell differentiation.
- In plants, growth is associated with both anabolic and catabolic activities. It is usually confined to meristems and involves an increase in size and number of cells.
- Thus we can say, growth is quantitative phenomenon and can be measured in relation to time.
- Growth involves following phenomenon-
    - Absorption of water
    - Absorption of solutes
    - Intussusceptions [Deposition of new wall materials on the stretched wall]
    - The relationship of growth of one part of an organism to another part is called allometry.
    - Growth involves different type of metabolic and genetic processes.

6.2 Definition

" The permanent and irreversible change in any dimension of an organism accompanying an increase in the dry weight is called growth."

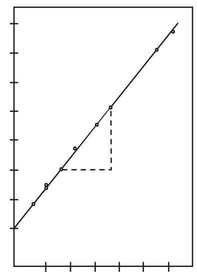
6.3 Plant growth and its regulators (Phytohormones)

- **Plant hormones** (also known as **phytohormones**) are chemicals that regulate plant growth, which, also termed as 'plant growth substances'.
- Plant hormones are signal molecules produced within the plant, and occur in extremely low concentrations.
- Hormones regulate cellular processes in targeted cells locally and when moved to other locations, in other locations of the plant.
- Hormones also determine the formation of flowers, stems, leaves, the shedding of leaves, and the development and ripening of fruit.
- Plants, unlike animals, lack glands that produce and secrete hormones; instead each cell is capable of producing hormones.
- Plant hormones shape the plant, affecting seed growth, time of flowering, the sex of flowers, senescence of leaves and fruits.
- They affect which tissues grow upward and which grow downward, leaf formation and stem growth, fruit development and ripening, plant longevity, and even plant death.
- Hormones are vital to plant growth and lacking them, plants would be mostly a mass of undifferentiated cells.

6.3.1 Growth Rate

- "The increased growth per unit time is termed as growth rate."
- Thus, rate of growth can be expressed mathematically. An organism or a part of the organism can produce more cells in a variety of ways.
- 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-



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

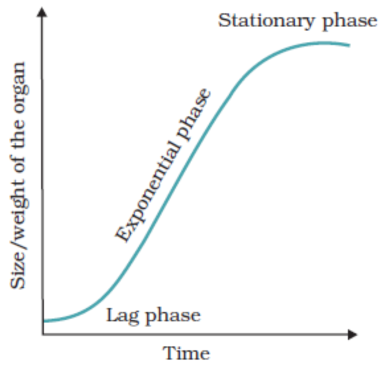
$L_t = L_0 + rt$ L_t = length at time't'

L_0 = length at time 'zero' r= growth rate / elongation per unit time.

6.3.2 Growth curves

"Sigmoid growth curve is a characteristic of living organism growing in a natural environment. It is typical for all cells, tissues and organs of a plant."

- In most systems, 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.



- A sigmoid growth curve typical of cells in culture, & many higher plants & plant organs.
- The exponential growth can be expressed as-

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

6.3.3 Conditions for Growth

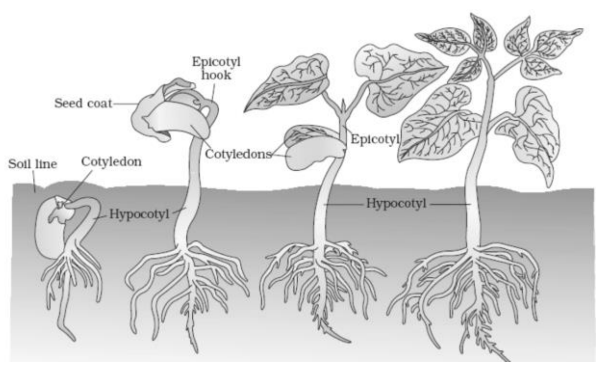
- As growth is brought about by cell division and cell elongation, the conditions necessary for growth are similar to that of synthesis of protoplasm and cell division.
- The supply of nutrients, water, oxygen suitable temperature and light are necessary for proper growth.
- The force of gravity and also light determines the direction of root and shoot growth.
- Nutrients provide essential materials for the synthesis of protoplasm and acts as a source of energy.
- Water maintains the turgidity of growing cells and provides medium for enzymatic reactions. Turgidity of cells helps in extension growth. Thus, plant growth and further development is intimately linked to the water status of the plant.
- Oxygen helps in releasing metabolic energy essential for growth activities.
- 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.
- Temperature above 45 ºC coagulates and damages the protoplasm and hinders growth.
- Environmental signals such as light and gravity also affect certain phases/stages of growth.
- Light is not essential during the initial stages of the growth, but it is required for further growth in photosynthesis. There is stimulating effect of light on plant growth, and its absence results in etiolation.
- Salts, mineral deficiencies and stress factors also influence the rate of growth.

6.3.4 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 develop very strong, elastic, lignocellulosic secondary cell walls, to carry water to long distances even under extreme tension.
- The living differentiated cells that by now 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.
- The growth in plants is open i.e. it can be indeterminate or determinate. It can be said because, cells/tissue 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. Example- cells positioned ahead of the root apical meristems differentiate as root-cap cells, while those pushed to the periphery mature as epidermis.

6.3.5 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. Diagrammatic representation of the sequence of processes which constitute the development of a cell of a higher plant is given in .It is also applicable to tissues/organs.
- Plants follow different pathways in response to environment or phases of life to form different kinds of structures.
- This ability is called plasticity, example- 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.
- 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.



Germination and seedling development in Bean

6.3.6 The Discovery of Plant Growth Regulators

- Charles Darwin and his son Francis Darwin when they observed that the coleoptiles of canary grass responded to unilateral illumination by growing towards the light source (phototropism).
- It was concluded that the tip of coleoptile was the site of transmittable influence that caused the bending of the entire coleoptile.
- Auxin was isolated by F.W. Went from tips of coleoptiles of oat seedlings.
- E. Kurosawa reported the appearance of the 'bakane' (foolish seedling) a disease of rice seedlings, was caused by a fungal pathogen *Gibberalla fujikuroi*.
- F. Skoog and his co-workers observed that from the internodal segments of tobacco stems the callus (a mass of undifferentiated cells) proliferated only if, in addition to auxins the nutrients medium was supplemented with one of the

following: extracts of vascular tissues, yeast extract, coconut milk or DNA. Skoog and Miller, later identified and crystallized the cytokinesis promoting active substance that they termed kinetin.

- During mid-1960s, three independent researchers reported the purification and chemical characterization 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).
- 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.

6.3.7 Introduction to 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.

6.3.8 Classes of Plant Growth Hormones

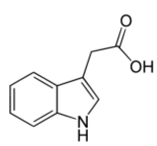
- In general, it is accepted that there are five major classes of plant hormones, some of which are made up of many different chemicals that can vary in structure from one plant to the other.
- The chemicals are each grouped together into one of these classes based on their structural similarities and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

- The five major classes are-
  - **Auxins**
  - **Gibberllins**
  - **Cytokinins**
  - **Abscisic Acid**
  - **Ehtylene**

6.3.9 Physiological effects of Auxins, Gibberllins, Cytokinins, Abscisic Acid and Ehtylene and their applications in agriculture and horticulture

6.3.9.1 Auxins

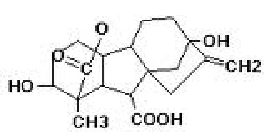
- Auxins are compounds that positively influence cell enlargement, bud formation and root initiation they the production of other hormones and in conjunction cytokinins,
- Auxins promote control the growth of stems, roots, and fruits and convert stems into flowers.
- They also were the first class of growth regulators discovered. They affect cell elongation by altering cell wall plasticity. Auxins decrease in light and increase where it is dark.
- Leaf abscission is initiated by the growing point of a plant ceasing to produce auxins. They act to inhibit the growth of buds lower down the stems and also to promote lateral and adventitious root development & growth.
- They stimulate cambium cells to divide and in stems cause secondary xylem to differentiate.
- Auxins are toxic to plants in large concentrations; they are most toxic to dicots and less so to monocots. Because of this property, synthetic auxin herbicides including 2,4-D and 2,4,5-T have been developed and used for weed control.
- Auxins in seeds regulate specific protein synthesis, as they develop within the flower after pollination, causing the flower to develop a fruit to contain the developing seeds.



- Auxins, especially 1-Naphthaleneacetic acid (NAA) and Indole-3-butyric acid (IBA), are also commonly applied to stimulate root growth when taking cuttings of plants.
- The most common auxin found in plants is indoleacetic acid or IAA. The correlation of auxins and cytokinins in the plants is a constant (A/C=const.)

6.3.9.2 Gibberllins

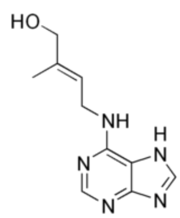
- Gibberellins or GAs were first discovered when Japanese researchers, including Eiichi Kurosawa, noticed a chemical produced by a fungus called *Gibberella fujikuroi* that produced abnormal growth in rice plants.



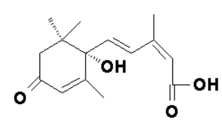
- Gibberellins are important in seed germination, affecting enzyme production that mobilizes food production used for growth of new cells. This is done by modulating chromosomal transcription.
- In grain (rice, wheat, corn, etc.) seeds, a layer of cells called the aleurone layer wraps around the endosperm tissue.
- Absorption of water by the seed causes production of GA. The GA is transported to the aleurone layer, which responds by producing enzymes that break down stored food reserves within the endosperm, which are utilized by the growing seedling.
- Gibberllic Acid promote flowering, cellular division, and in seeds growth after germination. Gibberellins also reverse the inhibition of shoot growth and dormancy induced by ABA.
- Gibberllic Acid produces bolting of rosette-forming plants, increasing internodal length.

6.3.9.3 Cytokinins

- The cytokinin zeatin, *Zea*, in which it was first discovered in immature kernels.
- Cytokinins or CKs are a group of chemicals that influence cell division and shoot formation. They were called kinins in the past when the first cytokinins were isolated from yeast cells.
- Cytokinins also help delay senescence or the aging of tissues, are responsible for mediating auxin transport throughout the plant, and affect internodal length and leaf growth.
- Cytokinins counter the apical dominance induced by auxins; they in conjunction with ethylene promote abscission of leaves, flower parts and fruits.



Cytokinin



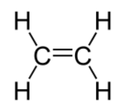
Abscisic Acid

6.3.9.4 Abscisic Acid

- Abscisic acid also called ABA, was discovered and researched under two different names before its chemical properties were fully known, it was called *dormin* and *abscicin II*.
- Once it was determined that the two latter compounds were the same; it was named abscisic acid.
- The name "abscisic acid" was given because it was found in high concentration in newly abscissed or freshly- fallen leaves.
- In plant species from temperate parts of the world it plays a role in leaf and seed dormancy by inhibiting growth, but, as it is dissipated from seeds or buds, growth begins.
- In other plants, as ABA levels decrease, growth then commences as gibberellin levels increase.
- Without ABA, buds and seeds would start to grow during warm periods in winter and be killed when it froze again.
- Since ABA dissipates slowly from the tissues and its effects take time to be offset by other plant hormones, there is a delay in physiological pathways that provide some protection from premature growth.
- It accumulates within seeds during fruit maturation, preventing seed germination within the fruit, or seed germination before winter.
- Abscisic acid's effects are degraded within plant tissues during cold temperatures or by its removal by water washing in out of the tissues, releasing the seeds and buds from dormancy.

6.3.9.5 Ethylene

- Ehtylene is a gaseous hormone, which stimulates transverse or isodiametric growth but retards the longitudinal growth.
- In 1935 Crocker et al discovered the presence of ethylene from the plant organs and named it as gaseous hormone.
- In 1970 Galston and Davis recognized Ehtylene as growth regulator.
- According to Denny and Miller (1935) Ethylene is formed in all plant parts roots, leaves, flowers, fruit, seeds. Maximum synthesis occurs during climacteric ripening of fruits and tissue undergoing senescence.
- Ethylene affects cell growth and cell shape; when a growing shoot hits an obstacle while underground, ethylene production greatly increases, preventing cell elongation and causing the stem to swell.

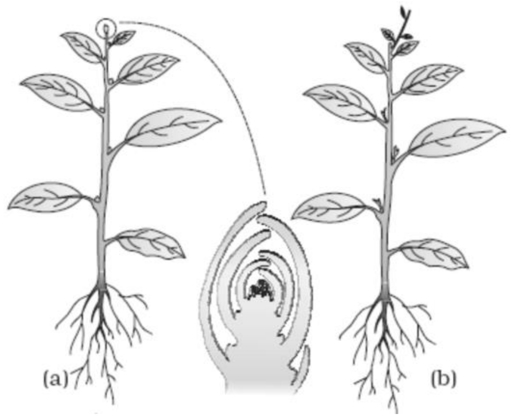


6.4 Phases of growth

- The period of growth is generally divided into three phases, namely, meristematic, elongation and maturation.
- In the root tips. 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.

6.5 Apical Dominance

- Apical dominance is the phenomenon whereby the main central stem of the plant is dominant over (i.e., grows more strongly than) other side stems; on a branch the main stem of the branch is further dominant over its own side branchlets.
- The apical bud (or tip) produces the growth hormone auxin, which not only promotes cell division, but also diffuses downwards and inhibits the development of lateral bud growth which would otherwise compete with the apical tip for light and nutrients.
- Removing the apical tip and its suppressive hormone allows the lower dormant lateral buds to develop and the buds between the leaf stalk and stem to produce new shoots which compete to become the lead growth.
- Manipulating this natural response to damage (known as the principle of apical dominance) by processes such as pruning (as well as coppicing and pollarding) allows the horticulturist to determine the shape, size and productivity of many fruiting trees and bushes.



Apical Dominance

6.6 Seed Dormancy

- **Seed dormancy** is a condition of plant seeds that prevents germinating under optimal environmental conditions. Living, non dormant seeds, germinate when soil temperatures and moisture conditions are suited for cellular processes and division, dormant seeds do not.
- Plant hormones affect seed dormancy by affecting different parts of the seed.
- Embryo dormancy is characterized by a high ABA/GA ratio, whereas the seed has a high ABA sensitivity and low GA sensitivity.
- True dormancy or innate dormancy is caused by conditions within the seed that prevent germination under normally ideal conditions.
- Often seed dormancy is divided into two major categories based on what part of the seed produces dormancy: exogenous and endogenous.
- There are three types of dormancy based on their mode of action: physical, physiological and morphological.

6.6.1 Exogenous dormancy

- Exogenous dormancy is caused by conditions outside the embryo and is often broken down into three subgroups-
  - Physical dormancy -Which occurs when seeds are impermeable to water or the exchange of gases.
  - Mechanical dormancy - Mechanical dormancy occurs when seed coats or other coverings are too hard to allow the embryo to expand during germination.
  - Chemical dormancy- Includes growth regulators etc, that are present in the coverings around the embryo.

6.6.2 Endogenous dormancy

- Endogenous dormancy is caused by conditions within the embryo itself, and it is also often broken down into three subgroups: physiological dormancy, morphological dormancy and combined dormancy, each of these groups may also have subgroups-
  - Physiological dormancy- Physiological dormancy prevents embryo growth and seed germination until chemical changes occur.
  - Morphological dormancy- Embryo underdeveloped or undifferentiated. Some seeds have fully differentiated embryos that need to grow more before seed germination, or the embryos are not differentiated into different tissues at the time of fruit ripening.
  - Combined dormancy- Seeds have both morphological and physiological dormancy.

6.6.3 Combinational dormancy

- Combinational dormancy occurs in some seeds, where dormancy is caused by both exogenous (physical) and endogenous (physiological) conditions.

6.6.4 Secondary dormancy

- Secondary dormancy occurs in some non-dormant and post dormant seeds that are exposed to conditions that are not favorable for germination, like high temperatures. It is caused by conditions that occur after the seed has been dispersed. The mechanisms of secondary dormancy are not yet fully understood but might involve the loss of sensitivity in receptors in the plasma membrane.

6.7 Senescence (Germination of Seed)

- Plant senescence is the study of aging in plants.
- Plants, just like other forms of organisms, seem to have both unintended and programmed aging.
- Leaf senescence is the cause of autumn leaf color in deciduous trees.

6.8 Fruit Ripening

- Ripening is a process in fruits that causes them to become more edible. In general, a fruit becomes sweeter, less green, and softer as it ripens. However the acidity as well as sweetness rises during ripening, but the fruit still tastes sweeter regardless. The reason for this is the Brix-Acid Ratio.
- Ripening agents speed up the ripening process.
- They allow many fruits to be picked prior to full ripening, which is useful since ripened fruits do not ship well. For example, bananas are picked when green and artificially ripened after shipment by being gassed with ethylene.
- A similar method used in parts of Asia was to cover a bed of slightly green-harvested mango and a few small open containers of clumps of calcium carbide with a plastic covering.
- The moisture in the air reacted with the calcium carbide to release the gas acetylene, which apparently has the same effect as ethylene.

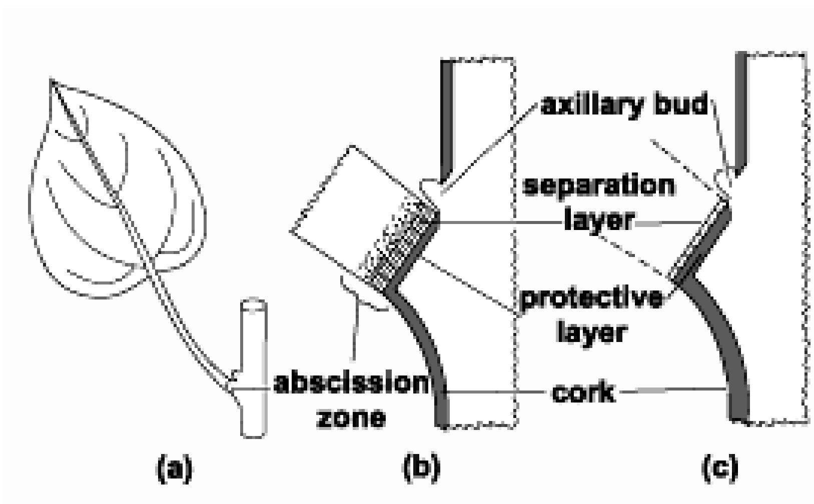
6.9 Abscission

"The fall of lateral organs like leaves from mature plants is called as abscission."

- It is shedding of leaves, branches, fruits, flowers etc. from the plants usually in response to hormonal changes.
- The hormones causing abscission are
  - Reduced titre of auxin
  - Increased level of ethylene
  - Increased level of abscisic acid

- In most plants, the abscising organs possess a basal swelling called abscission joint.
- In the abscission joint there is a strong development of parenchyma with weakly lignified tracheary elements and absence of sclerenchyma as well as collenchyma.
- Instead of abscission joint an abscission zone or region develops in others.
- It is distinguishable histologically from the remaining interior.
- Commonly an annular groove occurs on the outside and beginning of abscission zone.
- Instead of groove, the area may have band of different colour.
- Abscission zone differentiates into two parts, upper separation layer and lower protective layer. The various events which occur during abscission are as follows-

- **Conducting Elements**-The tracheary elements in and near the abscission zone get blocked by tyloses. This reduces the supply of water to abscising organ. There is loss of turgidity. The sieve tubes are also blocked temporarily by callose plugs to reduce supply of auxin and cytokinin. It sets in the process of senescence and accompanied degradation. Callose plugs later dissolve so that nutrients are drained out.
- **Separation Layer** – It develops at the upper end of abscission zone or joint in the area of annular groove. Development of separation layer may or may not involve cell division and cell enlargement. There is secretion of cellulase and polygalacturonase which result in dissolution of middle lamellae and weakening of cell walls. As a result the cells separate from those of upper part of the organ. Separation begins from periphery and proceeds towards the interior. They tracheary elements of separation layer also become weakened by the activity of cellulase and pectinase enzymes.
- **Protective Layer** – It consists of two parts-primary and secondary. The primary protective layer develops just below the separation layer by cicatrization or deposition of lignin, suberin or wound gum over the parenchyma cells. The secondary protective layer is formed by division of cells and their conversion into corky periderm. Protective layer is meant for protecting the plant from desiccation and pathogens in the area of abscission.
- **Abscission**-In perennial dicots and gymnosperms, development of separation layer proceeds centripetally. The vascular strand also weakens. As a result ,the organ falls down due to nonsupport. In most monocots and herbaceous dicots, abscission is accomplished more by physical stresses than enzymatic separation of cells.



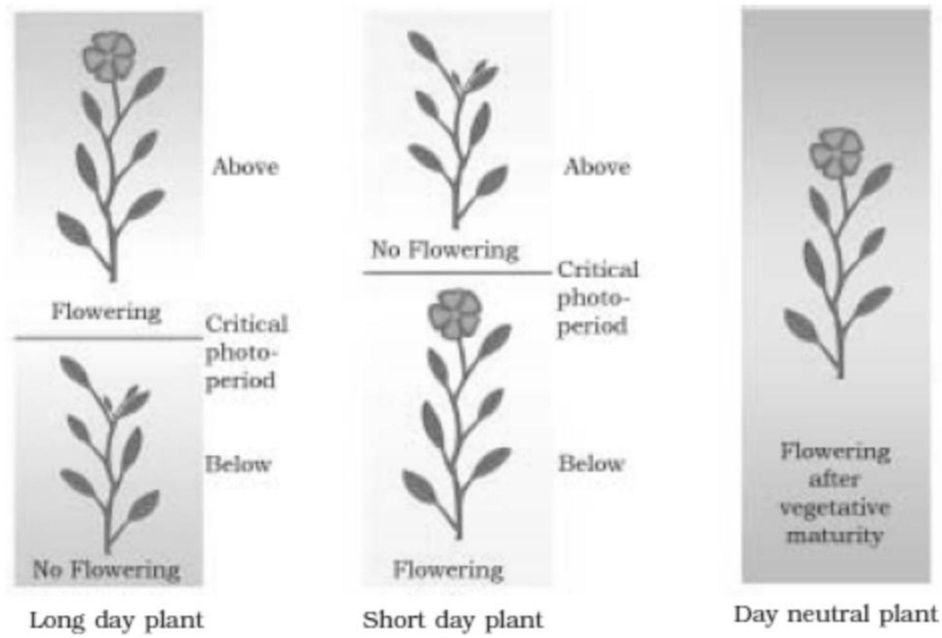
Diagrams of the abscission zone of a leaf.
(a) A leaf with the abscission zone indicated at the base of the petiole.
(b) The abscission zone layers shortly before abscission and
(c) the layers after abscission.

6.10 Plant Movements

- The concept of chemical messengers in plants emerged from a series of classic experiments on how stems respond to light.
- Plants grow toward light, and if you rotate a plant, it will reorient its growth until its leaves again face the light.
- Any growth response that results in curvature of whole plant organs toward or away from stimuli is called a **tropism.**
- The growth of a shoot toward light is called positive **phototropism;** growth away from light is negative phototropism.
- Much of what is known about phototropism has been learned from studies of grass seedlings, particularly oats.
- The shoot of a grass seedling is enclosed in a sheath called the coleoptile, which grows straight upward if kept in the dark or illuminated uniformly from all sides.
- If it is illuminated from one side, it will curve toward the light as a result of differential growth of cells on opposite sides of the coleoptile.
    - The cells on the darker side elongate faster than the cells on the brighter side.
- In the late 19th century, Charles Darwin and his son Francis observed that a grass seedling bent toward light only if the tip of the coleoptile was present.
- This response stopped if the tip was removed or covered with an opaque cap (but not a transparent cap).
- While the tip was responsible for sensing light, the actual growth response occurred some distance below the tip, leading the Darwin to postulate that some signal was transmitted from the tip downward.
- Later, Peter Boysen-Jensen demonstrated that the signal was a mobile chemical substance.
- He separated the tip from the remainder of the coleoptile by a block of gelatin, preventing cellular contact, but allowing chemicals to pass.
    - These seedlings were phototropic.
- However, if the tip was segregated from the lower coleoptile by an impermeable barrier, no phototropic response occurred.
    - In 1926, Frits Went extracted the chemical messenger for phototropism, naming it auxin.
    - Modifying the Boysen-Jensen experiment, he placed excised tips on agar blocks, collecting the hormone.
- If an agar block with this substance was centered on a coleoptile without a tip, the plant grew straight upward.
- If the block was placed on one side, the plant began to bend away from the agar block.
    - The classical hypothesis for what causes grass coleoptiles to grow toward light, based on the previous research, is that an asymmetrical distribution of auxin moving down from the coleoptile tip causes cells on the dark side to elongate faster than cells on the brighter side.
- However, studies of phototropism by organs other than grass coleoptiles provide less support for this idea.
- There *is,* however, an asymmetrical distribution of certain substances that may act as growth *inhibitors*, with these substances more concentrated on the lighted side of a stem.

6.11 Photoperiodism

- The appropriate appearance of seasonal events is of critical importance in the life cycles of most plants.
- These seasonal events include seed germination, flowering, and the onset and breaking of bud dormancy.



- The environmental stimulus that plants use most often to detect the time of year is the photoperiod, the relative lengths of night and day.
- A physiological response to photoperiod, such as flowering, is called **photoperiodism.**
- One of the earliest clues to how plants detect the progress of the seasons came from a mutant variety of tobacco studied by W. W. Garner and H. A. Allard in 1920.
- This variety, Maryland Mammoth, does not flower in summer as normal tobacco plants do, but in winter.
- In light-regulated chambers, they discovered that this variety would flower only if the day length was 14 hours or shorter, which explained why it would not flower during the longer days of the summer.
- Garner and Allard termed the Maryland Mammoth a **short-day plant,** because it required a light period *shorter* than a critical length to flower.
- Other examples include chrysanthemums, poinsettias, and some soybean varieties.

6.11.1 Long-day plants

- Long day plants will only flower when the light period is *longer* than a critical number of hours.
- Examples include spinach, iris, and many cereals.

6.11.2 Day-neutral plants

- Day –neutral plants will flower when they reach a certain stage of maturity, regardless of day length.
- Examples include tomatoes, rice, and dandelions.
- In the 1940s, researchers discovered that it is actually night length, not day length, that controls flowering and other responses to photoperiod.
- Research demonstrated that the cocklebur, a short-day plant, would flower if the daytime period was broken by brief exposures to darkness, but not if the nighttime period was broken by a few minutes of dim light.
- Short-day plants are actually long-night plants, requiring a minimum length of uninterrupted darkness.
- Cocklebur is actually unresponsive to *day* length, but it requires at least 8 hours of *continuous darkness* to flower.

- Similarly, long-day plans are actually short-night plants.
- A long-day plant grown on photoperiods of long nights that would not normally induce flowering will flower if the period of continuous darkness is interrupted by a few minutes of light.
- Long-day and short-day plants are distinguished *not* by an absolute night length but by whether the critical night lengths sets a maximum (long-day plants) or minimum (short-day plants) number of hours of darkness required for flowering.
- In both cases, the actual number of hours in the critical night length is specific to each species of plant.
- While the critical factor is night length, the terms "long-day" and "short-day" are embedded firmly in the jargon of plant physiology.
- Red light is the most effective color in interrupting the nighttime portion of the photoperiod.
- Action spectra and photoreversibility experiments show that phytochrome is the active pigment.
- If a flash of red light during the dark period is followed immediately by a flash of far-red light, then the plant detects no interruption of night length, demonstrating red/far-red photoreversibility.
- Plants measure night length very accurately.
- Some short-day plants will not flower if night is even one minute shorter than the critical length.
- Some plants species always flower on the same day each year.
- Humans can exploit the photoperiodic control of flowering to produce flowers "out of season."
- By punctuating each long night with a flash of light, the floriculture industry can induce chrysanthemums, normally a short-day plant that blooms in fall, to delay their blooming until Mother's Day in May.
- The plants interpret this as not one long night, but two short nights.
- While some plants require only a single exposure to the appropriate photoperiod to begin flowering, others require several successive days of the appropriate photoperiod.

6.12 Vernalisation

- Other plants respond to photoperiod only if pretreated by another environmental stimulus.
- For example, winter wheat will not flower unless it has been exposed to several weeks of temperatures below 10°C (called **vernalization**) before exposure to the appropriate photoperiod.
- While buds produce flowers, it is leaves that detect photoperiod and trigger flowering.
- If even a single leaf receives the appropriate photoperiod, all buds on a plant can be induced to flower, even if they have not experienced this signal.
- Plants lacking leaves will not flower, even if exposed to the appropriate photoperiod.
- The flowering signal, not yet chemically identified, is called **florigen,** and it may be a hormone or some change in the relative concentrations of two or more hormones.
- Whatever combination of environmental cues (such as photoperiod or vernalization) and internal signals (such as hormones) is necessary for flowering to occur, the outcome is the transition of a bud's meristem from a vegetative state to a flowering state.
- This requires that meristem-identity genes that induce the bud to form a flower must be switched on.
- Then organ-identity genes that specify the spatial organization of floral organs—sepals, petals, stamens, and carpels—are activated in the appropriate regions of the meristem.

- Identification of the signal transduction pathways that link external cues to the gene changes required for flowering are active areas of research.

6.13 Factors Affecting Growth

- The genotype of a plant affects its growth, for example selected varieties of wheat grow rapidly, maturing within 110 days, whereas others, in the same environmental conditions, grow more slowly and mature within 155 days.
- Growth is also determined by environmental factors, such as temperature, available water, available light, and available nutrients in the soil.
- Any change in the availability of these external conditions will be reflected in the plants growth.
- Biotic factors are also capable of affecting plant growth.
- Plants compete with other plants for space, water, light and nutrients.
- Plants can be so crowded that no single individual produces normal growth.
- Optimal plant growth can be hampered by grazing animals, suboptimal soil composition, lack of mycorrhizal fungi, and attacks by insects or plant diseases, including those caused by bacteria, fungi, viruses, and nematodes.
- Simple plants like algae may have short life spans as individuals, but their populations are commonly seasonal.
- Other plants may be organized according to their seasonal growth pattern: annual plants live and reproduce within one growing season, biennial plants live for two growing seasons and usually reproduce in second year, and perennial plants live for many growing seasons and continue to reproduce once they are mature.
- These designations often depend on climate and other environmental factors; plants that are annual in alpine or temperate regions can be biennial or perennial in warmer climates.
- Among the vascular plants, perennials include both evergreens that keep their leaves the entire year, and deciduous plants which lose their leaves for some part of it.
- In temperate and boreal climates, they generally lose their leaves during the winter; many tropical plants lose their leaves during the dry season.
- The growth rate of plants is extremely variable.
- Some mosses grow less than 0.001 millimeters per hour (mm/h), while most trees grow 0.025-0.250 mm/h.
- Some climbing species, such as kudz In temperate and boreal climates, they generally lose their leaves during the winter; many tropical plants lose their leaves during the dry u, which do not need to produce thick supportive tissue, may grow up to 12.5 mm/h.
- Plants protect themselves from frost and dehydration stress with antifreeze proteins, heat-shock proteins and sugars (sucrose is common).
- LEA (Late Embryogenesis Abundant) protein expression is induced by stresses and protects other proteins from aggregation as a result of desiccation and freezing.

6.14 Measurement of Growth

- 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.
- One single maize root apical meristem can give rise to more than 17,500 new cells per hour, whereas cells in a watermelon may increase in size by upto 3,50,000 times.
  In the former, growth is expressed as increase in cell number; the latter expresses growth as increase in size of the cell.

While the growth of a pollen tube is measured in terms of its length, an increase in surface area denotes the growth in a dorsiventral leaf.

6.15 Points to Remember

- Growth is one of the most conspicuous events in any living organism.
- It is an irreversible increase expressed in parameters such as size, area, length, height, volume, cell number etc.
- It conspicuously involves increased protoplasmic material. In plants, meristems are the sites of growth. Root and shoot apical meristems sometimes along with intercalary meristem, contribute to the elongation growth of plant axes.
- Growth is indeterminate in higher plants. Following cell division in root and shoot apical meristem cells, the growth could be arithmetic or geometrical.
- Growth may not be and generally is not sustained at a high rate throughout the life of cell/tissue/organ/organism.
- One can define three principle phases of growth– the lag, the log and the senescent phase.
- When a cell loses the capacity to divide, it leads to differentiation.
- Differentiation results in development of structures that is commensurate with the function the cells finally has to perform.
- General principles for differentiation for cell, tissues and organs are similar.
- A differentiated cell may dedifferentiate and then redifferentiate.
- Since differentiation in plants is open, the development could also be flexible, i.e., the development is the sum of growth and differentiation.
- Plant growth and development are under the control of both intrinsic and extrinsic factors.
- Intercellular intrinsic factors are the chemical substances, called plant growth regulators (PGR).
- There are diverse groups of PGRs in plants, principally belonging to five groups: auxins, gibberellins, cytokinins, abscisic acid and ethylene.
- These PGRs are synthesised in various parts of the plant; they control different differentiation and developmental events.
- Any PGR has diverse physiological effects on plants.
- Diverse PGRs also manifest similar effects.
- PGRs may act synergistically or antagonistically.
- Plant growth and development is also affected by light, temperature, nutrition, oxygen status, gravity and such external factors.
- Flowering in some plants is induced only when exposed to certain duration of photoperiod.
- Depending on the nature of photoperiod requirements, the plants are called short day plants, long day plants and day-neutral plants.
- Certain plants also need to be exposed to low temperature so as to hasten flowering later in life. This treatment is known as vernalisation.