CHAPTER-15

PLANT GROWTH AND DEVELOPMENT

Development is the sum of two processes: growth and differentiation. To begin with, it is essential and sufficient to know that the development of a mature plant from a zygote (fertilized egg) follows a precise and highly ordered succession of events. During this process, a complex body organization is formed that produces roots, leaves, branches, flowers, fruits, and seeds, and eventually, they die.

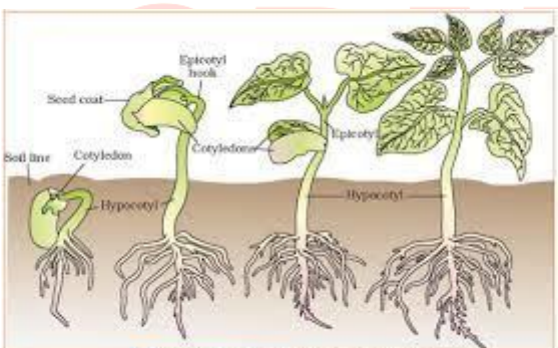


Fig: Germination and seedling development in bean

Some of the factors which govern and control these developmental processes. These factors are both intrinsic (internal) and extrinsic (external) to the plant.

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 the 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, for example, the expansion of a leaf is growth.

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 can divide and self-perpetuate. The product, however, soon loses the capacity to divide and such cells make up the plant body. 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 primary growth of the plants and principally contribute to the elongation of the plants along their axis. You also know that in dicotyledonous plants and gymnosperms, the lateral meristems, vascular cambium, and cork-cambium appear later in life. These are the meristems that an increase in the girth of the organs in which they are active. This is known as secondary growth of the plant.

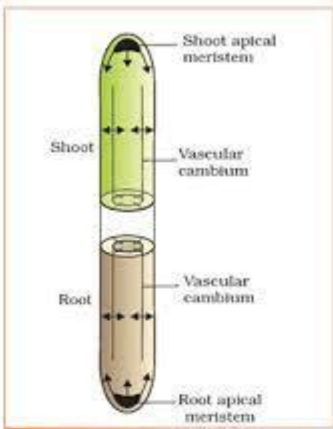
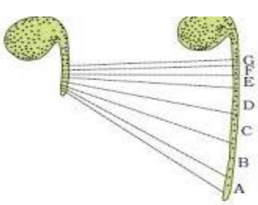


Fig: Diagrammatic representation of locations of root apical meristem, shoot aplical meristem and vascular cambium. Arrows exhibit the direction of growth of cells and organ.

Growth is Measurable

Growth, at a cellular level, is principally a consequence of the 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, and volume and cell number. It is amazing to know that one single maize root apical meristem can give rise to more than 17,500 new cells per hour, whereas cells in watermelon may increase in size by up to 3,50,000 times. In the former, growth is expressed as an increase in cell number; the latter expresses growth as an increase in the 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. Phases of Growth The period of growth is generally divided into three phases, namely, meristematic, elongation, and maturation.



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

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, thin, and cellulosic with abundant plasmodesmata 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 the 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

Primary Growth: Apical meristems of roots and shoots is responsible for the primary growth

Secondary Growth: Secondary growth is due to lateral meristems, e.g. vascular and cork cambium. The plant increases in the girth due to secondary growth

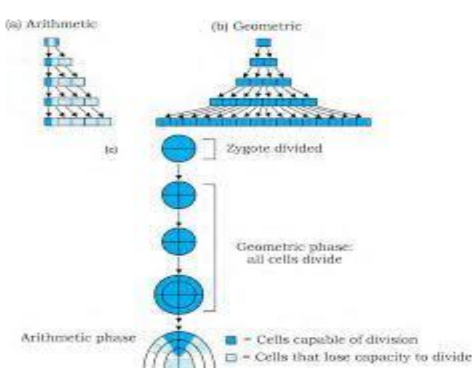
Phases of Growth: There are three phases of growth:

Meristematic (formative phase) growth is shown by apices of roots and shoots. The meristematic growth is facilitated by a thin cellulosic cell wall, along with many plasmodesmata connections

Elongation (phase of enlargement) is characterized by deposition in the cell wall and increased vacuolation

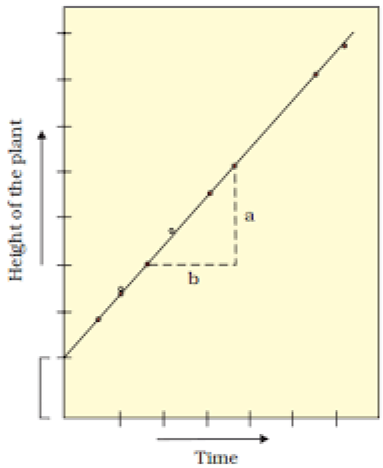
Maturation is characterized by cell wall thickening and lignification. Cells attain maturity and their maximal size and undergo protoplasmic modifications.

The increased growth per unit time is termed as growth rate. Thus, the 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,

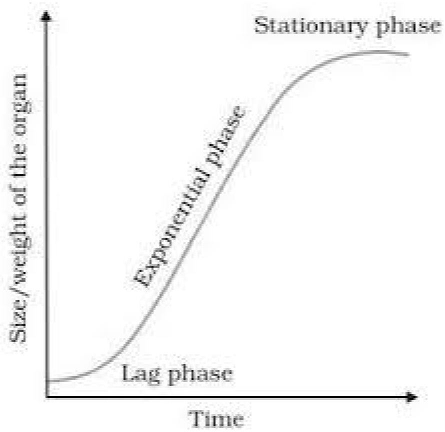
It is expressed as

$L_t = L_0 + rt$

L_t = length at time 't'

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

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 organisms growing in a natural environment. It is typical for all cells, tissues, and organs of a plant.

The exponential growth can be expressed as

$W1 = W_0\ ^{ert}$

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

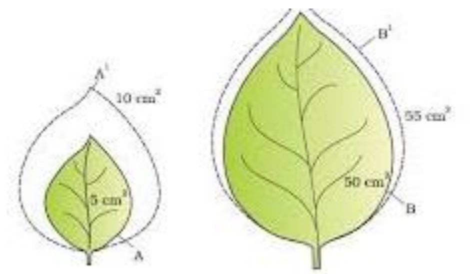
e = base of natural logarithms

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 the efficiency index. Hence, the final size of W_1 depends on the initial size, W_0.

Growth	Mathematical expression	Curve
In Arithematic growth : Only one daughter cell continues to divide mitotically while other differentiates and matures.	$L_t = L_0 + rt$ L_t = Length at time t L_0 = Length at time zero r = growth rate	Linear curve
In geometrical growth : The initial growth is slow (lag phase) and increase rapidly there-after at an exponential rate (log phase). • Both the progeny cells divide mitotically and continue to do so. However, with limited nutrient supply, the growth slow down leading to stationary phase.	$W_1 = W_0 e^{rt}$ W_1 = Final size W_0 = Initial size r = growth rate t = time of growth e = base of natural logarithms	Sigmoid or S-curve

Quantitative comparisons between the growth of the 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.

The two leaves, A and B, are drawn that are of different sizes but shows an absolute increase in area in the given time to give leaves, A1 and B1.



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

The necessary conditions for growth can be listed as water, oxygen and nutrients as 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 are 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 a source of energy.

Also, 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 develop very strong, elastic, lignocellulosic secondary cell walls, to carry water too long distances even under extreme tension. Try to correlate the various anatomical features you encounter in plants to the functions they perform. Plants show another interesting phenomenon. The living differentiated cells, that by now have lost the capacity to divide can regain the capacity of the division under certain conditions. This phenomenon is termed as dedifferentiation.

For example, the formation of meristems – interfascicular cambium and cork cambium from fully differentiated parenchyma cells. While doing so, such meristems/tissues can 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. Now, it may be said 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 the 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. Diagrammatic representation of the sequence of processes which constitute the development of a cell of a higher plant.

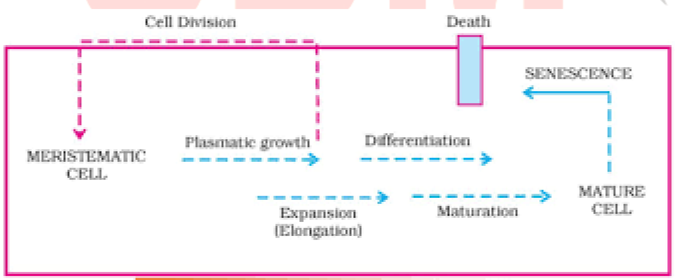
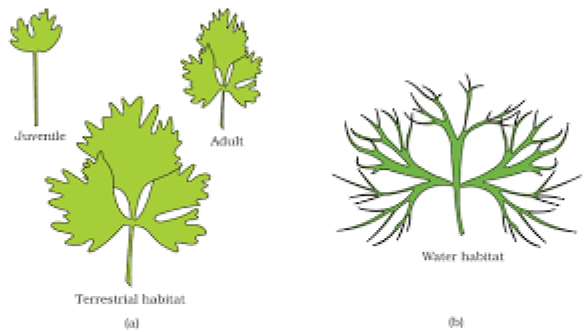


Fig: Sequence of the developmental process in a plant cell

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, 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, the difference in shapes of leaves produced in air and those produced in water in buttercup also represent the heterophyllous development due to environment



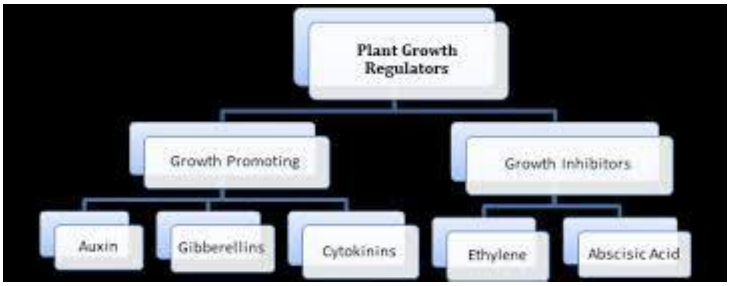
This phenomenon of heterophylly is an example of plasticity.

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 include 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 (N6 -furfurylamino purine, kinetin), derivatives of carotenoids (abscisic acid, ABA); terpenes (gibberellic acid, GA3) 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 have 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 plays 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.



According to their actions, they can be classified into two categories:

Plant growth promoters, which induce cell division, elongation, differentiation and the formation of flowers, fruits and seeds, e.g. auxins, gibberellins, cytokinins.

Plant growth inhibitors are linked to dormancy, abscission and various stress responses, e.g. Abscisic acid (ABA).

Ethylene, the gaseous hormone has inhibitory as well as growth-promoting effects.

Brassinosteroids also have been discovered to work as a phytohormone.

Different plant hormones may work antagonistically or complimentary (synergistically) to each other. Many events get affected by more than one phytohormones, such as apical dominance, dormancy, abscission, senescence, etc.

The Discovery of Plant Growth Regulators

Interestingly, the discovery of each of the five major groups of PGRs has been accidental. All this started with the observation of 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). After a series of experiments, it was concluded that the tip of coleoptile was the site of transmittable influence that caused the bending of the entire coleoptile.

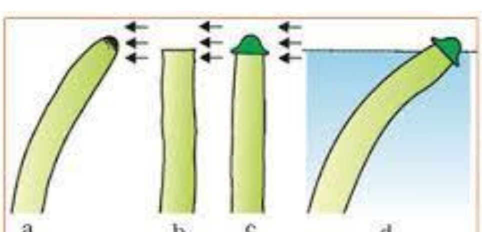


Fig: Experiment used to demonstrate that tip of the coleoptile is the source of auxin. Arrows indicate direction of light

Auxin was isolated by F.W. Went from tips of coleoptiles of oat seedlings.

The 'bakane' (foolish seedling) disease of rice seedlings, was caused by a fungal pathogen Gibberella fujikuroi. E. Kurosawa reported the appearance of symptoms of the disease in uninfected rice seedlings when they were treated with sterile filtrates of the fungus. The active substances were later identified as gibberellic acid. 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 crystallised the cytokinesis promoting active substance that they termed kinetin. During the mid-1960s, three independent types of research reported the purification and chemical characterisation of three different kinds of inhibitors: inhibitor-B, abscission II and domain. 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.

Physiological Effects of Plant Growth Regulators

Auxins

Auxins (from Greek 'auxin': to grow) was first isolated from human urine. The term 'auxin' is applied to the indole-3-acetic acid (IAA), and 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 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.

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.

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.

Gibberellins

Gibberellins are another kind of promoter PGR. There are more than 100 gibberellins reported from widely different organisms such as fungi and higher plants. They are denoted as GA1, GA2, GA3 and so on. However, Gibberellic acid (GA3) was one of the first gibberellins to be discovered and remains the most intensively studied form. All GAs are acidic. They produce a wide range of physiological responses in the plants. Their ability to cause an increase in the length of the axis 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 to extend the market period. GA3 is used to speed up the malting process in the 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 promote bolting (internode elongation just before 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. leaves, chloroplasts in leaves, lateral shoot growth and adventitious shoot formation. Cytokinins help overcome 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 the ripening of the fruits. This rise in the 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 deepwater 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 a 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.

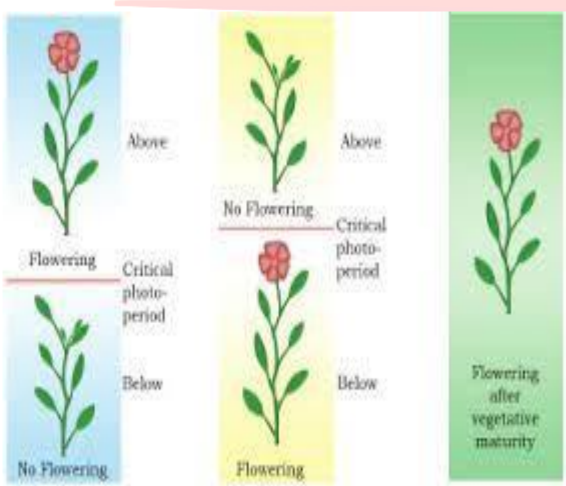
Abscisic acid

The abscisic acid (ABA) was discovered for its role in regulating abscission and dormancy. But like other PGRs, it also has other wide-ranging effects on plant growth and development. 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. We may summarise that for any and every phase of growth, differentiation and development of plants, one or the other PGR has some role to play. Such roles could be complementary or antagonistic. These could be individualistic or synergistic.

Similarly, there are some 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. Remember, 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

It has been observed that some plants require a periodic exposure to light to induce flowering. It is also seen that such plants can 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.



It is now also known that not only the duration of the light period but that the duration of the 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 before flowering, they (i.e., shoot apices of plants) by themselves cannot perceive photoperiods. The site of perception of light/dark duration is 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 especially 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 is 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 overwinter 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. Sugarbeet, 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.

Important terms

Abscission
Shedding of plant organs like leaves, flowers and fruits etc. from the mature plant.

Apical dominance
Suppression of the growth of lateral buds in the presence of apical bud.

Dormancy
A period of suspended activity and growth usually associated with low metabolic rate.

Photoperiodism
The response of the plant to the relative length of day and night period to induce flowering.

Phytochrome
A pigment, which controls the light-dependent developmental process.

Phytohormone
Chemicals secreted by plants in minute quantities which influence the physiological activities.

Senescence
The last phase of growth when metabolic activities decrease.

Vernalisation
A method of promoting flowering by exposing the young plant to low temperature.

Growth
An irreversible permanent increase in the size of an organ or its parts or even of an individual. Abbreviations IAA Indole acetic acid NAA Naphthalene acetic acid ABA Abscisic acid IBA Indole-3 butyric acid 2.4D 2.4 dichloro phenoxy acetic acid PGR Plant growth regulator

Measurement of growth
Plant growth can be measured by a variety of parameters like increase in fresh weight, dry weight, length, area, volume and cell number.

Phases of growth
The period of growth is generally divided into three phases, namely, meristematic, elongation and maturation.

Meristematic zone
The new cell produced by metotic division at root-tip and shoot tip thereby show an increase in size. Cells are rich in protoplasm and nuclei.

Elongation zone

Zone of elongation lies just behind the meristematic zone and concerned with enlargement of cells.

Maturation zone

The portion lies proximal to the phase of elongation. The cells of this zone attain their maximum size in terms of wall thickness and protoplasmic modification.

Growth rate

The increased growth per unit time is termed as growth rate. The growth rate shows an increase that may be arithmetic or geometrical.

Differentiation

A biochemical or morphological change in the meristemic cell (at root apex and shoot apex) to differentiate into the permanent cell is called differentiation.

Dedifferentiation

The phenomenon of regeneration of permanent tissue to become meristematic is called dedifferentiation.

Redifferentiation

Meristems/tissue can produce new cells that once again lose the capacity to divide but mature to perform specific functions.

Growth promoting hormones

These are involved in growth-promoting activities such as cell division, cell enlargement, flowering, fruiting and seed formation. e.g., Auxin, gibberellins, cytokinins. Growth inhibitor: Involved in growth-inhibiting activities such as dormancy and abscission. e.g., Abscisic acid and Ethylene.