

PLANT GROWTH AND DEVELOPMENT

GROWTH

- Growth is a characteristic of life. Every living organism shows growth which can either be in size or in number. It can be indefinite or determinate.
- Growth is defined as a permanent or irreversible increase in dry weight, size, mass or volume of a cell, organ or organism. During growth, anabolic processes exceed catabolic processes or growth is final end product of successful metabolism. Growth is intrinsic in living beings. Unlike animals, plants do not stop growing after reaching maturity. They continue to grow and bear new roots, leaves, branches, flowers, etc. While roots, stems and their branches have indefinite growth, other organs like leaves, flowers and fruits show limited or definite growth.
- In multicellular plants growth is restricted to some specific region (called meristems). The growing region in plants are apices of shoot and root where meristems are present.

Phases of growth

- Plant growth takes place in three steps or phases—formative phase, enlargement phase and differentiation phase.
- **Formative phase or cell division phase** (cells of apical meristem divide) is the first phase of growth which occurs in areas where meristematic cells are present, e.g., shoot tip, root tip. Formative phase represents the lag phase of growth.
- **During enlargement phase or cell elongation phase** proteins, protoplasm, cell wall material is synthesized and the newly formed cells, produced in the formative phase, undergo enlargement.
- **Differentiation phase or cell maturation phase** (secondary walls are laid down) occurs further behind the phase of elongation. The enlarged cells develop into special or particular type of cells by undergoing structural and physiological differentiation.

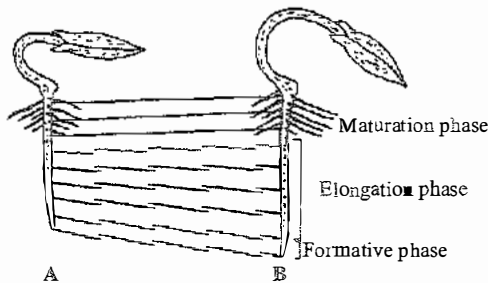


Fig.: Phases of growth. A, marked radicle in the beginning. B, marked radicle at the end.

Types of growth

- Growth can be of two types: Arithmetic or geometric.
 - Arithmetic growth** : It is a type of growth in which the rate of growth is constant and increase in growth occurs in arithmetic progression i.e., 2, 4, 6, 8 etc. Here after mitosis, only one daughter cell continues to divide. Other takes part in differentiation and maturation. Here a linear curve is obtained with positive value.

(ii) **Geometric growth** : It is quite common in unicellular organisms when grown in nutrient rich medium. Here, every cell divides. The daughters grow and divide. The grand daughters repeat the process and so on. Initial growth is slow as the number of cells initially are small. Later on, there is rapid growth at exponential rate. It is called log or exponential growth. An embryo initially shows geometrical growth in cells, but later it passes into arithmetic phase.

Growth rates

- The expression of increased growth per unit time is called **growth rate**.
- The **rate of growth** can be measured by an increase in size or area of an organ of the plant like leaf, flower, fruit etc. in a unit time. The rate of growth is also called **efficiency index**.
- Measurement and comparison of total growth per unit time is called **absolute growth rate**.
- The growth of the given system per unit time expressed per unit initial parameter is called **relative growth rate**.

$$\frac{\text{Growth in given time period}}{\text{Measurement at time of start period}}$$

- Suppose two leaves have grown by 5 cm² in one day. Initial size of leaf A was 5 cm² while that of leaf B was 50 cm². Though their absolute growth is the same (5 cm²/day), relative rate of growth is faster in leaf A (5/5) because of initial small size than in leaf B (5/50).

Growth curve

- It is the graphic representation of the total growth against time.
- Depending upon the growth pattern growth curves can be of following types:
 - **Arithmetic growth curve**: If length of a plant showing arithmetic growth is plotted against time the graph obtained is called arithmetic growth curve. Usually linear graph is obtained. e.g., length of a plant is measured as 2, 4, 6, 8, 10, 12 cms at a definite interval of 24 hrs. It is found in root or shoot elongating at constant rate. Arithmetic growth is expressed as $L_t = L_0 + rt$.
 - Here, L_t = length after time t . L_0 = length at the beginning, r = growth rate.

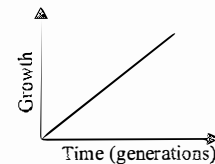


Fig.: Arithmetic growth curve

- **Geometric growth curve**: Geometric growth is the growth where both the progeny cells following mitosis retain the ability to divide and continue to do so. It occurs in many higher plants and in unicellular organisms when grown in nutrient rich medium. Number of cells is initially small so that initial growth is slow which is called lag phase. Later on, there is rapid growth at exponential rate. It is called log or exponential phase.

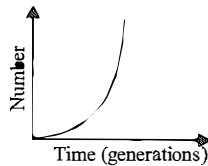


Fig.: Geometric curve

- The exponential growth curve can be represented by equation : $W_1 = W_0 e^{rt}$
where W_1 is final size (weight, height, number etc.)
 W_0 = Initial size at the beginning of the time period.
 r = growth rate
 t = time of growth
 e = base of natural logarithms (2.71828).
- Practically, in living organisms geometric growth curve is not observed because growth depends upon nutrition and it does not show a steady increase. As a result sigmoid growth curve is obtained.
- Sigmoid growth curve** : Geometric growth cannot be sustained for long. Some cells die. Limited nutrient availability causes slowing down of growth. It leads to stationary phase. There may be actually a decline. Plotting the growth against time will give a typical sigmoid or S-curve.

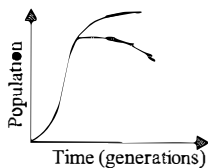


Fig.: Sigmoid growth curve

- S-curve of growth is typical of most living organisms in their natural environment. It also occurs in cells, tissues and organs of plants.
- If total growth is plotted against time, an S-shaped or **sigmoid curve** is obtained. It consists of four parts – lag phase, log phase (exponential phase), phase of diminishing growth and stationary phase (steady growth for organs or organisms of indefinite growth).
- Growth is **slow in the lag phase, rapid during log or exponential phase, slow again during the phase of diminishing growth. Growth stops completely during the stationary phase.** Log phase is also called **grand phase of growth** by Sachs (1873).

Measurement of growth

- Growth is measured by measuring increase in length, (e.g., stem, root, pollen tube), increase in volume, (e.g., fruits), increase in area, (e.g., leaves), increase in diameter, (e.g., tree trunks, fruits), or increase in fresh or dry weight. Growth is measured with the help of **auxanometer** (arc auxanometer and Pfeffer's auxanometer), **horizontal microscope** and **crescograph**, (a sensitive apparatus for measuring growth, developed by Sir. J.C. Bose).

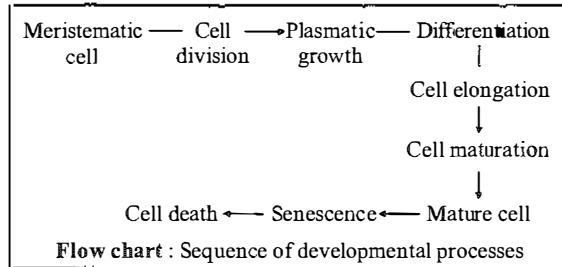
Factors or conditions affecting growth

- The growth of a plant is influenced by the intensity, quality, duration and direction of **sunlight**. Plant growth is greatly influenced by **temperature**. **Water** is extremely essential for maintaining the vital physiological processes in plants and also for maintaining the turgidity of cells.

- Sufficient supply of **nutrients** cause an increase in the rate of anabolic processes which dominates over the rate of catabolic processes. As a result, **growth** occurs. The rate of photosynthesis depends on **carbon dioxide** concentration. **Oxygen** is invariably required for the living cells, to respire. However, for growth, **optimum** concentration of oxygen is desirable as higher concentration of oxygen sometimes retards the growth rate.

DEVELOPMENT

- Development is the sequence of changes that occurs in the structure and functioning of an organism, organ, tissue or cell involving its formation, growth, differentiation, maturation, reproduction, senescence and death.



- The ability to change under the influence of internal or external stimuli is called **plasticity**. The **intrinsic plasticity** is found in cotton, coriander. Environmental plasticity is best seen in emergent hydrophytes like buttercup (*Ranunculus flabellaris*). In both cases plants show heterophylly. **Heterophylly** is the occurrence of different types of leaves on the same plant habitually in different growth phases or under different environmental conditions.

Differentiation

- Differentiation is the permanent qualitative change in structure, chemistry and physiology of cell wall and protoplasm of cells, their tissues and organs. It is caused by repression of some genes.

Dedifferentiation

- Dedifferentiation is the process of despecialization of differentiated living cells so that they regain the capacity to divide and form new cells. A dedifferentiated tissue can act as meristem, e.g., interfascicular vascular cambium, cork cambium, wound cambium.

Redifferentiation

- Redifferentiation is the structural, chemical and physiological specialisation of cells derived from dedifferentiated meristematic cells. Secondary phloem, secondary xylem, cork, secondary cortex are some of the tissues formed through redifferentiation.

PHYTOHORMONES OR GROWTH REGULATORS

- A plant hormone or **phytohormone** is a chemical substance produced naturally in plants which is translocated to another region for regulating one or more physiological reactions when present in low concentration. As growth regulators can also be external factors like nutrients etc. So **all phytohormones are growth regulators but all growth regulators are not phytohormones.** Phytohormones are of

two types: **growth promoters** (e.g., auxins, gibberellins and cytokinins) and **growth inhibitors** (e.g., abscisic acid and ethylene).

Auxins

- The very existence of growth substances was proposed by **Charles Darwin** (1880) in his book *The Power of Movements in Plants*. While working on canary grass (*Phalaris canariensis*), he demonstrated that apical tips of seedlings are sensitive to unilateral illumination and show positive phototropism. He concluded that the tip senses the unilateral light stimulus but the curvature occurs lower down as a result of more rapid growth on the shaded than illuminated side of the coleoptile. He also noted that when tip of coleoptile was excised no curvature response occurred.
- Thus he showed that the growth of shoots towards light was the result of some 'influence' being transmitted from the shoot tip to the region of growth behind it.
- **F.W. Went** was the first person to name these substances of tip as auxins (Greek *auxein* means 'to grow').
- Auxins are made continuously in the shoot apex and young leaves. **Tryptophan** is the precursor of IAA and zinc is responsible for its synthesis. IAA is the example of natural auxin. **Important bioassays of auxins are :**
 - *Avena* curvature test.
 - Rice root inhibition test.

Role of auxins

- Auxins induce **cell division** activity in cambium and **elongation** of cells in shoot. Auxins induce early **differentiation** of xylem and phloem in tissue culture experiment. In general, auxins initiate rooting but inhibit the growth of roots. IBA is the most potent root initiator
- Auxins inhibit the growth of axillary buds and promote **apical dominance**. **Thimann** and **Skoog** reported that IAA (auxin) is responsible for apical dominance.
- Auxins enhance the size of carpel and hence **earlier fruit formation**. Application of auxins **retards the process of senescence** (last degradative phase). Application of auxins retards the abscission of leaves, fruits, branches, etc.
- Auxins induce **parthenocarpic development** of fruits and such fruits are seedless.
- Auxins induce **feminisation**, i.e., on male plant, female flowers are produced.
- **2,4-D** is a famous herbicide or **weedicide** (especially kills broad leaved weeds). It kills weeds perhaps by over stimulated root growth.
- Auxins are responsible for **phototropism and geotropism**.
- Mixture of 2,4-D and 2,4, 5-T (dioxin) is given the name '**Agent Orange**' which was used by U.S.A. in Vietnam war for defoliation of forests (i.e., in chemical warfare).

Gibberellins

- Gibberellin is very important plant hormone, which was first of all reported in Japan, where a disease in rice called '**bakane disease**' or '**foolish seedling disease**' spread, in which rice plants became abnormally long with significant internodal elongation. It was first reported by Japanese that

there is some connection between bakanae disease and fungus *Gibberella fujikuroi* (*Fusarium moniliformae*).

- **Sawada** reported that this bakanae disease is caused by a chemical secreted by the fungus *Gibberella fujikuroi* and later it was supported by **Kurosawa**. **Yabuta and Sumuki** finally isolated and crystallized these chemicals and named them as gibberellic acids or gibberellins (GA₃). Acetyl CoA is the precursor of gibberellins.
- **Bioassays of GA₃ are :**
 - Dwarf maize leaf sheath elongation bioassay
 - Barley half seed endosperm test or α -amylase bioassay.

Role of gibberellins

- GA enhances seed germination by enhancing α -amylase synthesis and thus **overcomes dormancy**. In photoblastic seeds (e.g., lettuce), seed germination occurs by application of GA even in dark.
- When GA is sprayed on rosette plants, there is rapid expansion of internodes and flowers with long stalks are produced. This phenomenon is called **bolting**. If GA is sprayed on single gene dwarf plant, **genetic dwarfism is overcome** and plant becomes long, e.g., in maize and pea, etc.
- On female plant, male flowers are produced by application of GA.
- Gibberellic acids are more potent parthenocarpic agents than auxins.

Cytokinins

- Cytokinins (*Cytos-cell ; Kinesis-* division) are hormones that promote cell division in plants. **F. Skoog and Miller** (1955) discovered that **autoclaved DNA from herring sperm** stimulated cell division in tobacco pith cells. They called the cell division inducing principle as kinetin (6-furfuryl amino purine). This does not occur in plants.
- In 1963, **Letham** introduced the term **cytokinin**. **Letham and Miller** (1964) isolated and identified a new cytokinin called **zeatin** (6-hydroxy 3 methyl trans 2 - butenyl amino purine). This was isolated from the unripe grains of maize.
- **Bioassays of cytokinins are :**
 - Chlorophyll retention test.
 - Root inhibition test.

Role of cytokinins

- Cell division activity is enhanced by cytokinins. Cytokinins control **initiation of plant organs**, i.e., morphogenesis.
 - High cytokinin/auxin ratio – Differentiation of shoot.
 - Low cytokinin/auxin ratio – Differentiation of root.
 - Intermediate cytokinins/auxin ratio – Differentiation of both root and shoot.
 - Intermediate cytokinin/low auxin – Callus formation.
- Application of cytokinins increases seedling growth in width.
- Cytokinins **overcome apical dominance** even in presence of apex.

- **Induction of female flowers** in male plants. **Retards senescence** (Richmond-Lang effect).
- **Retards abscission. Mobilization of food material** is increased by application of cytokinins and this is the reason of release of apical dominance by cytokinins.
- **Integrity of membranes and retention of chlorophyll.**

Abscisic Acid (ABA)

- ABA is regarded as one of the principle accelerators of abscission and bud dormancy. Chemically it is 15-C compound and is having 3 isoprene units. It is naturally occurring growth inhibitor in plants and also known as **stress hormone**. It was first isolated by Carns and Addicott.
- **Bioassays of abscisic acid are :**
 - Rice seedling growth inhibition test
 - Inhibition of α -amylase synthesis in barley endosperm test.

Role of ABA

- ABA is an active substance inducing abscission of different plant parts. Seed germination is limited and hence **induces dormancy** of seeds and buds.
- ABA inhibits flowering in long day plants but stimulates flowering in short day plants.
- ABA causes **partial closure of stomata under drought** and thus acts as **antitranspirant**. Hence also known as **stress hormone**.
- Leaves make large amount of ABA during drought and this ABA functions as messenger that enables plants to conserve water during drought.
- **Senescence** of leaf is promoted by ABA.
- ABA **counteracts many effects of GA** such as induction of hydrolases and α -amylase in barley seedlings.

Ethylene

- Ethylene is the only gaseous phytohormone. It is a growth inhibitor. Ethylene is mainly concerned with maturation and fruit ripening. It is a volatile gas formed by the complete combustion of carbon rich substances like coal, petroleum, etc. Crocker *et al.* (1935) identified ethylene as natural plant hormone.
- **Bioassays of ethylene are :**
 - Triple pea test.
 - Pea stem swelling test.

Role of ethylene

- Seed germination is promoted and hence overcomes dormancy.
- External supply of very small quantity of ethylene increases the number of female flowers and hence fruits in cucumber. Thus induces feminisation.
- Ethylene promotes abscission and senescence of leaves, flowers, etc.
- Ethylene shows triple response as its application **checks vertical growth, plumule or nodes become swollen** and leads to horizontal growth. Ethylene initiates adventitious root formation but retards the growth of roots.

- **Ripening and maturity of fruits** are two basic properties of this hormone. When applied as foliar spray ethylene accelerates maturity and induces uniform ripening.

SEED GERMINATION

- A seed may be defined as, “the fertilized integumented megasporangium”. After fertilization, ovules develop into seeds. The activation and growth (rejuvenation) of the embryo into a seedling during favourable conditions is called germination.

Types of germination

- There are two methods of seed germination epigeal and hypogeal. During **epigeal germination**, cotyledons are pushed out of the soil. This happens due to the elongation of the hypocotyl. *E.g.*, castor, bean, *Ricinus*. During **hypogeal germination**, cotyledons do not come out of the soil but remain under ground. Hypocotyl does not elongate. *E.g.*, maize, pea, millets, gram, coconut.
- **Vivipary** is said to occur when seeds germinate *in situ*, *i.e.*, seedling is formed even when the fruit is still attached to the mother plant. This is also called **aerial germination**. *E.g.*, mangroves (*Rhizophora*).
- Seeds of most of the plants usually do not require **light** for germination. However, seeds of epiphytes, *Ficus aurea*, *Digitalis purpurea*, etc. require light for germination. On the other hand light prevents seed germination in onion, *Phoenix* etc. Seeds which germinate only in presence of light are called **photoblastic** seeds.
- Internal factors affecting germination are state of embryo, dormancy, inability etc. A seed germinates only when the embryo inside it attains **maturity**.
- The capacity of a seed to germinate and develop into a seedling is called **seed viability**. **Seed vigour** is the ability of a seedling to establish itself in the soil and lead independent life. Many seeds require a **dormancy** or **resting period** after harvesting and germinate only after resting period.

SEED DORMANCY

- Dormancy may be defined as, “the inactive state of the seed in which growth of the embryo is temporarily suspended for a specific length of time”.

Causes of dormancy

- Seed coats of some plants like mustard, *Lepidium* (pepper grass) etc., are very **tough**. The growing embryo fails to emerge out due to the resistance of the **thick seed coat**.
- Seed coats of some seeds may be **impermeable** either to water (seeds of malvaceae, leguminosae, achenes of *Nelumbium*) or oxygen (seeds of compositae – *Xanthium*). As a result, seeds remain dormant.
- **Immature** or (rudimentary) incompletely developed embryo, at the time of shedding causes seed dormancy.
- Seeds of apple, peach etc. contain fully developed (mature) embryos by the time they are shed. But these seeds fail to germinate even if favourable conditions are provided because they contain **dormant embryo**.
- **Dormancy** of this type is due to **physiological immaturity** of the embryo. Such seeds undergo “after ripening” in nature and then only germinate.

Breaking of dormancy

- After the onset of specific conditions, seed dormancy is broken. Dormancy of seed can break naturally or it can be induced artificially. There are numerous reasons of breaking of seed dormancy after some time, such as:
 - Seeds with immature embryo germinate only when their embryo becomes mature, e.g., *Eranthis*.
 - Tough and impermeable seed coats become weakened and rupture by mechanical abrasions during dispersal.
 - Seeds lying in the soil are attacked by microbes which weaken their seed coats.
 - Passage through digestive tract is important in breaking seed dormancy in some seeds. Small seeds of edible fruits pass through the digestive tract of animals. HCl and digestive enzymes present inside the animal digestion tract weaken the seed coats.
 - Wetting of seeds during rains result in leaching of inhibitors present in the seed coats and pericarps.
 - Oxidation of inhibitors with passage of time is an important factor controlling seed dormancy.
 - Slowly the embryo synthesises growth hormones. They not only overcome growth inhibitors but also create conditions favourable for seed germination.
 - Artificially, it can be done by (i) vigorous shaking, (ii) pressure of about 2000 bars, (iii) mechanical rupturing (mechanical scarification), (iv) chemical scarification or (v) chilling treatment, etc.

VERNALISATION

- Term vernalisation was first given by T. D. Lysenko. Vernalisation is the process of shortening of the juvenile or vegetative phase and hastening flowering by a previous cold treatment. In vernalisation by cold treatment winter varieties are transferred into spring or summer varieties.
- Site of vernalisation is apical meristem or all the meristematic cells, e.g., shoot tip, embryo tips, root apex, etc. As a result of vernalisation, a flowering hormone called vernalin is formed (reported by Melchers), but vernalin has never been isolated. Once a plant is vernalised, it can be de-vernalised by exposing the plant to temperature of 30°C or above. For establishing vernalisation, plant should be kept at 20°C for 4-5 days.

Conditions necessary for vernalisation

- Age of the plant suitable for vernalization varies from plant to plant, e.g., in wheat, vernalization is done in germinating seeds.
- Temperature of 1–6°C is the optimum temperature.

Importance of vernalisation

- Vernalisation has following advantages:
 - Crops can be grown earlier. Juvenile or vegetative period is shortened and brings about early flowering.
 - Plants can be grown in such regions where normally they do not grow.
 - Yield of the plant is increased.

- Resistance to cold and frost is increased.
- Resistance to fungal diseases is increased.

PHOTOPERIODISM

- The effect of photoperiods or daily duration of light hours (and dark periods) on the growth and development of plants, especially flowering, is called photoperiodism. Photoperiodism was first studied by Garner and Allard (1920) in 'Maryland mammoth'.
- Long Day Plants (LDPs) flower when they receive long photoperiods or light hours which are above a critical length, e.g., henbane (*Hyoscyamus niger*), wheat, oat, sugar beet, spinach (*Spinacea oleracea*), radish, barley, larkspur, lettuce.
- Short Day Plants (SDPs) flower in photoperiods less than critical day length, e.g., *Nicotiana tabacum*, *Glycine max* (soybean), *Xanthium* (cocklebur), *Canabis sativa*, etc.
- Day Neutral Plants (DNPs) are insensitive to the day length. They flower at about the same time under all day lengths but can be promoted by night or low temperature or by a temperature alteration, e.g., *Curcumis sativus*, *Gossypium hirsutum*, *Pisum sativum*, etc.
- Long Short Day Plants (L-SDP). The plants require long photoperiods for floral initiation and short photoperiods for blossoming. The plants flower between summer and autumn, e.g., *Bryophyllum*, *Cestrum*.
- Intermediate Day Plant (IDP): The plants flower within a definite range of light hours. Flowering does not take place above and below this range, e.g., Wild Kidney Bean.

Critical day length

- A short day plant (SDP) flowers only when it receives a long dark period and short photoperiod, e.g., *Xanthium*, *Dahlia* etc. On the other hand, a long day plant (LDP) will flower only when it receives a long photoperiod and short dark period, e.g., wheat, oat etc. Thus critical photoperiod is that continuous duration of light which must not be exceeded in SDP and should always be exceeded in LDP in order to bring them to flower.
- But in some conditions a LDP and SDP can flower simultaneously, e.g., *Xanthium* requires light for less than 15.6 hrs and henbane requires light for more than 11 hrs. *Xanthium* (a SDP) and henbane (LDP) will flower simultaneously in light period between 11 to 15.6 hrs.

Significance of photoperiodism

- Photoperiodism determines the season in which a particular plant shall flower. For example, short day plants develop flowers in autumn-spring period (e.g., *Dahlia*, *Xanthium*) while long day plants produce flowers in summer (e.g., *Amaranthus*).
- Knowledge of photoperiodic effect is useful in keeping some plants in vegetative growth (many vegetables) to obtain higher yield of tubers, rhizomes etc. or keep the plant in reproductive stage to yield more flowers and fruits.
- A plant can be made to flower throughout the year by providing favourable photoperiod.
- It helps the plant breeders in effective cross-breeding in plants.
- Enables a plant to flower in different seasons.

Photoperiodic perception

- Photoperiodic stimulus is picked up by the fully developed leaves (Knott, 1934). Even one leaf or a part of it (upto 1/8) is sufficient for this purpose. Very young or first few leaves (7 leaves in *Xanthium strumarium*) are commonly insensitive. However, in *Pharbitis nil* (Japanese Morning Glory and *Chenopodium rubrum* (Pigweed) even the cotyledons can perceive the stimulus.
- **Borthwick and Hendricks** (1952) reported a photoreceptive pigment called "**phytochrome**". It is a bright blue or bluish

green pigment which was first of all isolated from plasma membrane of alga *Mougeotia*.

- The chemical which perceives the photoperiodic stimulus in leaves is **phytochrome**.
- Red, far red exposures given in succession show that plant response is determined by the last exposure. It is found that photoperiodic response is mediated by phytochrome which shows reversible change in red (660 nm) and far-red (730 nm) wavelength.

