

BSC 2.2

Growth and development of horticultural crops

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**BSC 2.2 GROWTH AND DEVELOPMENT OF HORTICULTURAL CROPS
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Growth and development- definition, component, different stages of growth, growth curves, growth analysis in horticultural crops. leaf area index (LAI)- optimum LAI in horticultural crops, canopy and photosynthetic productivity, Plant bioregulators- auxin, gibberellin, cytokinin, ethylene inhibitors and retardants, basic functions, biosynthesis, role in crop growth and development, propagation, flowering, fruit setting, fruit thinning, fruit development, fruit drop and fruit ripening. Flowering – factors affecting flowering, physiology of flowering, photoperiodism- long day, short day and day neutral plants, vernalisation and its application in horticulture. Pruning and training- physiological basis of training and pruning, source and sink relationship, translocation of assimilates. Physiology of seed development and maturation, seed dormancy and bud dormancy, causes and breaking methods in horticultural crops. Physiology of fruit growth and development, fruit setting, factors affecting fruit set and development, physiology of ripening of fruits- climacteric and non climacteric fruits.

Suggested Reading:

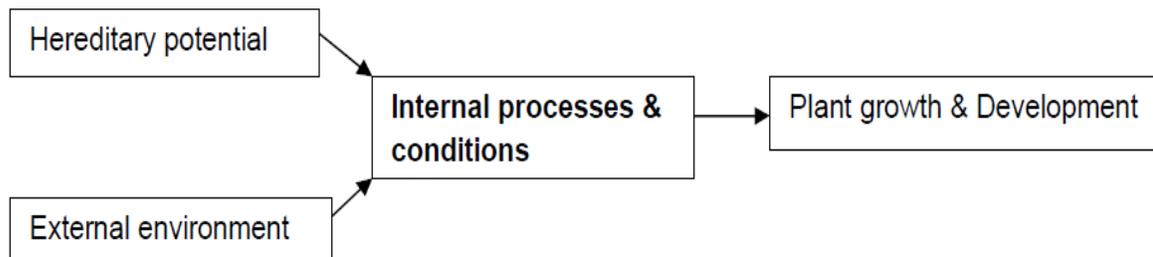
- ! Plant physiology by *Pandey and Sinha*
- ! Physiology of Crop Plants by *Franklin P. Gardner, R. B Pearce, R.L Mitchell*
- ! Plant growth and development by *A Carl Leopold*

Why we need to understand crop growth and development?

Modern agricultural science relies to increase crop production by maximizing growth and yield potential of crop plants. This achieves through both genetic and environmental manipulation. Genotypes can be changed by plant breeding and selection. The microclimate (environment near the plant surface) can be altered in many ways such as site selection, tillage, irrigation, fertilization and other cultural practices. Most of these cultural practices used to manipulate plant growth so that we can increase productivity. Thus it is essential to understand crop growth and development so that we can manipulate the growth pattern as per our need.

Plant and Animal growth and development:

Plant cells are not mobile during development due to a cell wall. In animals, determination and differentiation occurs in the embryo. Growth in plants is restricted to certain zones,



recently produced by cell division in a **meristem**. It is easy to confuse growth (as defined above as an increase in size) with cell division in meristems. Cell division alone does not cause increased size, but the cellular products of division also increase in volume and cause growth. Root and shoot tips (**apices**) are meristematic in nature. In plants, cells in the meristems keep dividing and the newly formed cells keep differentiating throughout the life of the plant. This means that different parts of the same plant are of different ages.

Determination and differentiation of plant cells is much more **plastic** than animals. Application of hormones, wounding or other treatments result in plant cells altering pathways of development to form different tissues and organs.

Plant cells are **totipotent** (in other words a single, non germ-line cell can be induced to regenerate to a whole organism), a property not generally seen in animals. This implies that the entire genome of that cell is intact and functional and that it can be brought back to an embryonic state.

Growth and Development:

Growth is irreversible increase in dry weight or size due to cell division and subsequent cell enlargement. Growth includes assimilation and the formation of new protoplasm, permanent change in size and increase in weight either of the plant as a whole or of some organ or tissue.

Development is defined as an ordered change or progress, often towards a higher, more ordered or more complex state.

Development may take place with growth and growth may take place with development. Growth leads to the development. However, these two processes are often linked together and occur in sequence. Growth is a quantitative change in contrast to development which is more of a qualitative change. Plant growth and development are essential processes of life and propagation of a species. Plant growth is the results of genotype and environment (internal and external) interaction. Certain traits in a plant are influenced by genotype, others by environment; the degree of each depends on the particular trait. DNA codes the sequencing of amino acids into specific proteins and enzymes, resulting in whole plant body architecture.

Growth and differentiation:

Plant development is a combination of complex processes of growth and differentiation that leads to an accumulation of dry matter. While growth is the increment in weight or volume due to cell division and cell enlargement, differentiation is the formation of specialized cells like xylem and phloem and formation of different plant parts like root, stem, leaves, etc.

Differentiation processes have three requisites

- i. Available assimilates in excess of most metabolic uses
- ii. A favourable temperature
- iii. Proper enzyme system for cell wall thickening, secondary product accumulation (eg. alkaloids and starches) and protoplasm hardening may occur which result in changes in anatomy and morphology.

Factors affecting growth:

External factors:

1. Climate factors : light, temperature, water, day length, wind and gases
2. Edaphic factors : texture, structure, organic matter, nutrient availability, pH, cation exchange capacity and salinity, alkalinity, acidity condition,
3. Biological factors : weeds, insects, diseases, soil microbes etc

Internal Factors:

1. Resistance to biotic and abiotic stress
2. Photosynthetic rate
3. Partitioning of assimilates
4. Type and location of meristems
5. Capacity to store food reserves
6. Enzyme activity
7. Direct gene effects (eg. hybrids)

Some Definitions:

Determinate and Indeterminate Plant: Plants in which vegetative and reproductive growth are distinct i.e. occur in separate time period. e.g. Wheat, rice are termed as determinate type while plants in which vegetative and reproductive growth run simultaneously known as indeterminate plants e.g. Chilli, Tomato

Monocarpic and polycarpic plants: Plants which flower only once and then die are termed as monocarpic eg. Annuals

Plants which flower and return to vegetative mode of growth and flower at least once before dying are termed as polycarpic plants.

Most monocarpic species are annuals. However, some of them are biennials and perennials also. Many varieties of bamboos may grow and live for over 50 years and then they flower and die. Thus bamboos are perennial but monocarpic. All polycarpic plants are perennials. Though a monocarpic species, it would be called a perennial because it lives for more than two growing seasons. Polycarpic plants, perennials by definition, do not convert all their vegetative meristems to determinate reproductive ones. Woody perennials (shrubs and trees) may use only some of their axillary buds for the formation of flowers, keeping the terminal buds vegetative; alternatively, terminal buds may flower while axillary buds remain vegetative.

Vegetative and reproductive growth:

In annuals, vegetative growth is generally terminated by reproduction. Leaves, stems and other vegetative parts not only fail to compete for current assimilate during ripening of fruits but also sacrifice previously accumulated carbon and minerals through mobilization and redistribution.

Perennials make only partial commitment to reproduction, and shoot that bear fruits may remain healthy and new vegetative shoots are generated from axillary buds.

REGIONS OF GROWTH:

Plant growth not occur in all tissues but it occur in specialized tissues known as **meristems** which are discrete regions or groups of cells that possess continued cell division for the life of the plant or that organ.

Based on location in the plant body, meristem can be classified into the following three types

Apical Meristem

It is the meristem present at the tip of the root and stem, commonly called as root apex and shoot apex respectively. Such meristems constitute the actively growing regions in the plant body. Due to the activity of apical meristem the plant body keeps increasing in its length.

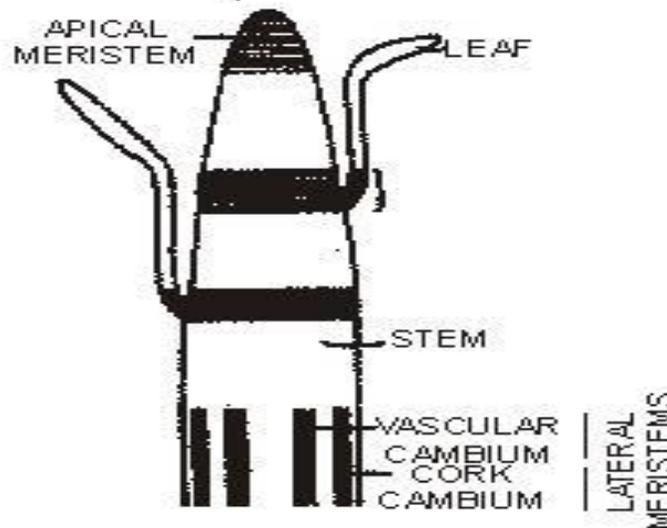
Intercalary Meristem

It is the meristem that occurs between permanent tissues. It represents the remnant of the apical meristem. It is particularly common at the nodal regions. It may also occur at the base of the leaves. The intercalary meristem also contributes towards the increase in length as it

brings about elongation of the internodal regions. It is also responsible for the formation of branches at the nodal regions.

Lateral Meristem

It is the meristem that occurs laterally, parallel to the long axis of plant body. Cambium strips formed in the vascular bundles and in the cortex are common examples of lateral meristem. It is responsible for an increase in the girth (circumference) of the plant body as it brings about the formation of secondary permanent tissues.



Different types of meristem

The root and shoot apical meristems are formed during embryo development, while the seed develops and are called **primary meristems**. The vascular cambium and the meristematic zones of monocot nodes and grass leaves are indistinguishable until after germination; they are **secondary meristems**.

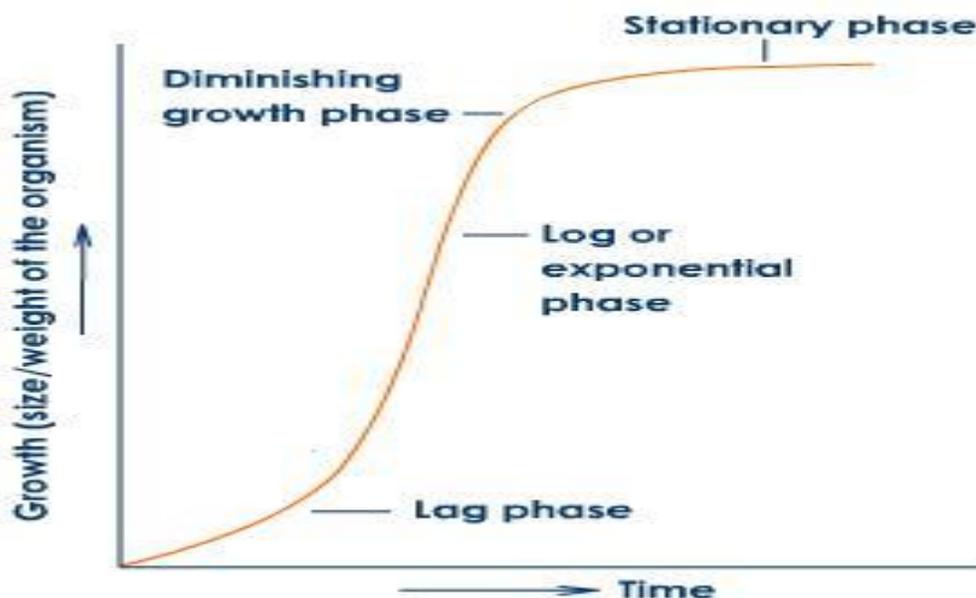
KINETICS OF GROWTH - THE COURSE OF GROWTH (GRAND PERIOD OF GROWTH) OR SIGMOID CURVE (GRAND PERIOD CURVE) AND PATTERN OF GROWTH:

Growth in plants is generally limited to regions of growing points known as **meristems**. The two important growing points present in the root apex and stem apex are called **apical meristems** and growth due to them is known as primary growth. The formation of tissues of a plant, the increase in the length of the plant and the differentiation of various appendages are due to the primary growth.

In certain kinds of plants e.g., bamboo, mint, increase in length is also due to **intercalary meristems**. These are actually a part of the apical meristems which get separated from the apex by the intervening permanent tissues. These meristems are of a temporary nature. A third type of growing point is known as the **lateral meristems**, which is responsible for the thickness of the plant in girth. This is called secondary growth. Here

meristematic cells, in the form of cambium are present in the vascular bundles of root and stem, thus increasing their thickness.

Growth of a plant is usually measured in terms of increase in dry weight, length or height and such measurement indicate that growth rate varies with age of the plant. The total time during which this course of growth takes place is called as the **Grand period of Growth**. If this growth rate is plotted against time, a slanting S shaped curve is obtained which is called as **Sigmoid Curve or Grand Period Curve**. A relatively slow growth rate characterizes early or seedling growth. The rate of growth increases as the plant become larger, is greatest just before or in early stages of flowering and then decreases as plant matures.



During the initial stage, i.e., during the lag phase, the rate of plant growth is slow. This phase is followed by a period of exponential growth rate in which rate of growth increases rapidly. After some time the growth rate slowly decreases due to limitation of nutrients. This phase constitutes the stationary phase.

In unicellular organisms such as bacteria, growth is assessed by a count of number of cells per milliliter at increasing times after the cells are placed in a fresh nutrient medium and under environmental conditions (light, temperature, etc.) suitable for optimal growth. Here also, there is initial lag period during which cells activate their biochemical machinery for rapid growth by synthesizing necessary enzymes. This is followed by a time period during which there is exponential increase in cell number which is called as **log period**. This period of rapid growth does not continue indefinitely and due to depleted nutrient supply, accumulation of toxic products and other limiting factors ultimately leads to **decreasing cell number** until the population of cells reaches a **steady state** in which the number of cells remains **constant (stationary) or even declines**.

GROWTH PATTERN OF ANNUAL CROPS:

Here the first phase relates to the seed germination and seedling growth. Seeds germinating below ground are dependent on stored material in the cotyledons until the seedling emerges in to light and start photosynthesis. Hence, initial increase in weight is negligible. (**LAG PHASE**)

The second phase of growth is characterized by a rapid and often linear increase in dry matter production and terminates with flowering (anthesis). (**LOG PHASE**)

It is associated with tillering, stem elongation and leaf expansion in cereals. In case of **indeterminate crops** such as Cotton, Pigeon pea etc. it is characterized by formation of branches with large number of leaves. Initiation of flower buds signifies end of rapid growth phase (**grand period of growth**) and indicates onset of flowering. The third phase of growth is marked by a reduction in growth rate until growth ceases at maturity. Assimilates stored in leaves and stems are translocated to partially sustain seed growth. At the end of this growth period, water is lost from aerial plant parts, photosynthesis stops and crop ripens (**STATIONARY PHASE AND DEATH**).

MEASUREMENT OF PLANT GROWTH:

Growth can be measured by a variety of parameters as follows:

A. Fresh Weight

Determination of Fresh weight is an easy and convenient method of measuring growth. For measuring fresh weight, the entire plant is harvested, cleaned for dirt particles if any and then weighed.

B. Dry Weight

The dry weight of the plant organs is usually obtained by drying the materials for 21 to 48 h at 70 to 80°C and then weighing it. The measurements of dry weight may give a more valid and meaningful estimation of growth than fresh weight. However, in measuring the growth of dark grown seedling it is desirable to take fresh weight.

C. Length

Measurement of length is a suitable indication of growth for those organs which grow in one direction with almost uniform diameter such as roots and shoots. The length can be measured by a scale. The advantage of measuring length is that it can be done on the same organ over a period of time without destroying it.

D. Area

It is used for measuring growth of plant organs like leaf. The area can be measured by a graph paper or by a suitable mechanical device. Nowadays modern laboratories use a photoelectric device (digital leaf area meter) which reads leaf areas directly as the individual leaves are fed into it.

GROWTH ANALYSIS:

Frequently, we need to know more than the end result i.e final yield of dry matter. The environment prevailed during the whole growth season markedly influence on

final outcome. Approach to the analysis of yield influencing factors and plant development as net photosynthate accumulation is naturally integrated over time has been known as growth analysis. Only two measurements made at frequent intervals, are required for growth analysis: leaf area and dry weight. Other quantities in the analysis are derived by calculation.

Advantages of growth analysis

- a) We can study the growth of the population or plant community in a precise way with the availability of raw data on different growth parameters.
- b) These studies involve an assessment of the primary production of vegetation in the field i.e. at the ecosystem level (at crop level) of organization.
- c) The primary production plays an important role in the energetics of the whole ecosystem.
- d) The studies also provide precise information on the nature of the plant and environment interaction in a particular habitat.
- e) It provides accurate measurements of whole plant growth performance in an integrated manner at different intervals of time.

Growth Parameters

Leaf Area Index (LAI): Watson (1947) proposed the term leaf area index which is the ratio of the leaf area of a plant to the ground area occupied by the plant.

$$\text{Leaf area index} = \frac{\text{Total leaf area of the plant}}{\text{Ground area occupied by the plant (spacing)}}$$

Leaf Area Duration (LAD) : It is ability of the plant to maintain the green leaves per unit area of the land over a period of time. It reflects the vitality of leaves and an opportunity for assimilation. It also measures the persistence of the assimilating surface.

$$\text{LAD} = \frac{L_1 + L_2}{2} \times (t_2 - t_1)$$

- Where L_1 – Leaf area index at first stage
- L_2 - Leaf area index at second stage
- $t_2 - t_1$ – Time interval between the two consequent stages and expressed in days.

Crop Growth Rate: The dry matter accumulation per unit of land area is referred as crop growth rate (CGR), normally expressed as $\text{g. m}^{-2}.\text{day}^{-1}$. CGR is measured by harvesting plants at frequent intervals and calculating the increase in dry weight from one sampling to the next. Roots are generally excluded from the studies.

$$\text{CGR} = 1/\text{GA.} (W_2 - W_1) / (T_2 - T_1)$$

- Where GA is plant ground area
- W_2 and W_1 is dry weight at T_2 and T_1 days

Maximum CGR occurs when plants are large enough to exploit all the environmental resources to the greatest degree. It occur when leaf cover is complete and maximum rate of

solar energy conversion for a given species at a given period of time. CGR analysis is important to explain yield differences among crop varieties and cultural practices.

Relative Growth rate (RGR):

Relative growth rate is the increased in plant dry weight per unit dry weight already present and expressed as $g \cdot g^{-1} \cdot day^{-1}$ at any instant during growth.

$RGR = (\ln W_2 - \ln W_1) / (T_2 - T_1)$ where \ln is Log_e (e base = 2.71828)

RGR decreases with plant age due to the fact that an increasing part of the plant is structural rather than photosynthetically active tissue and as such does not contribute to growth and impart to shading and increased age of lower leaves.

Net Assimilation Rate (NAR) :

Net assimilation rate (NAR) is a measure of the average efficiency of leaves on a plant or in a crop stand or dry matter accumulation rate per unit of leaf area. When all leaves are exposed to full sunlight NAR remains highest. It also remains highest when plants are small and leaves are few enough that none are shaded by others. As plants grow more and more leaves are full or partially shaded, thus NAR decreases during the growing season and with plant's age due to low photosynthetic efficiency of older average leaf with increasing respiratory tissues, NAR decreases. NAR expressed in $g \cdot cm^{-2} \cdot d^{-1}$

$NAR = (W_2 - W_1) / (T_2 - T_1) \times (\ln LA_2 - \ln LA_1) / (LA_2 - LA_1)$

Where W_2 and W_1 is dry weight of plant at T_2 and T_1 time period

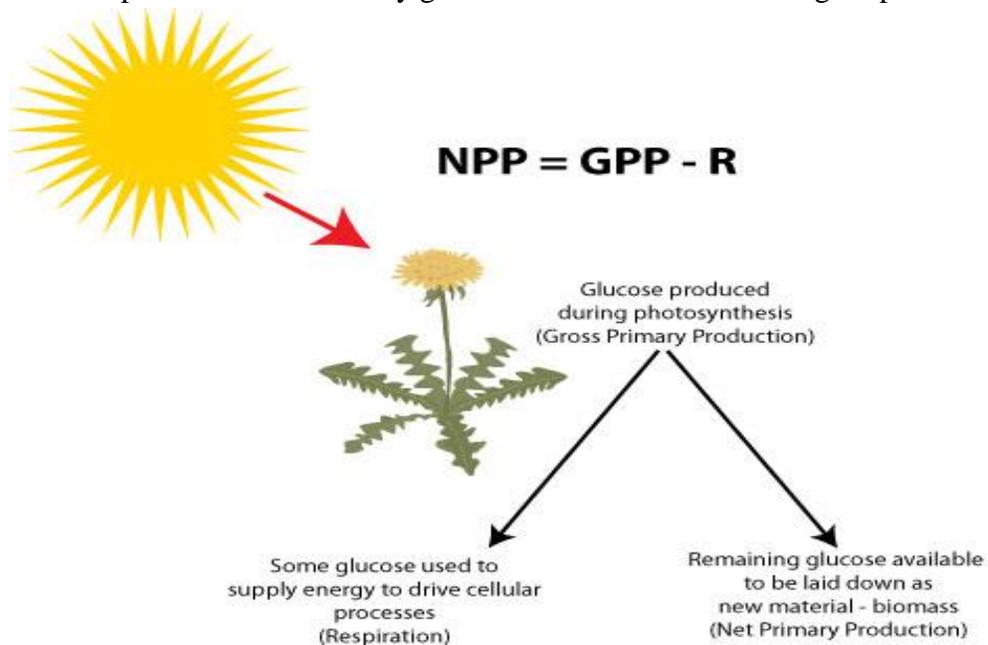
LA_2 and LA_1 are leaf area at T_2 and T_1 time period

Where \ln is Log_e (e base = 2.71828)

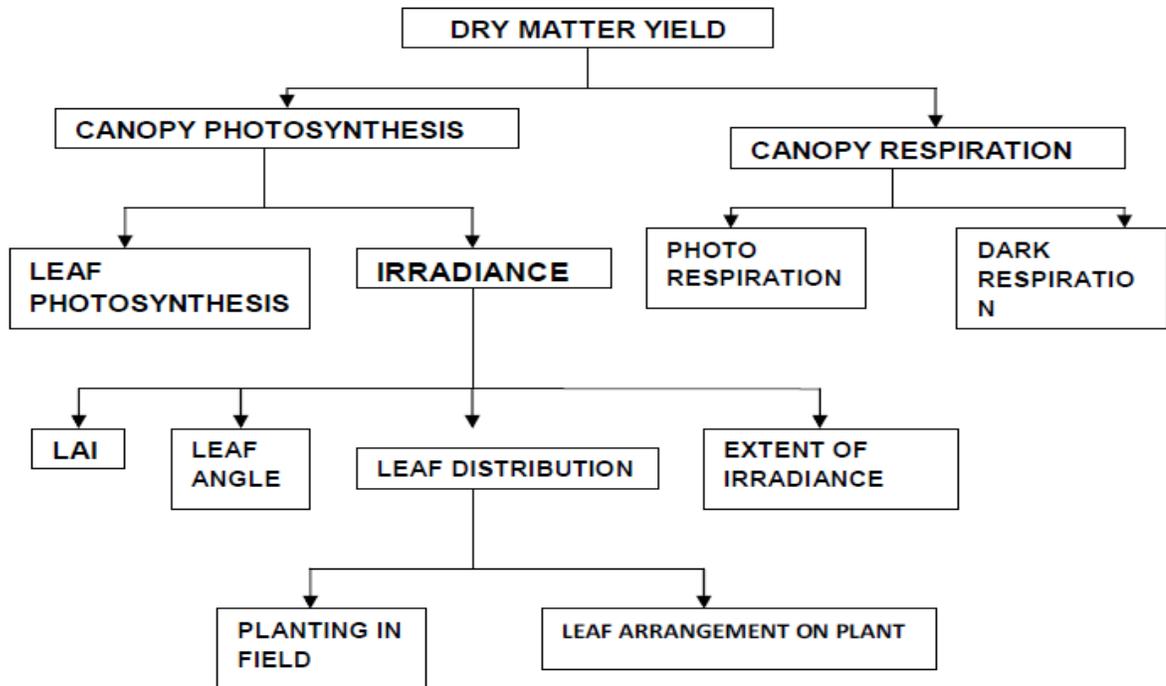
CANOPY PHOTOSYNTHESIS AND PRODUCTIVITY:

Productivity is the accumulation of matter and energy in biomass. Primary productivity is performed by green plants which are the only organism capable of capturing solar energy and converting it into the chemical energy of carbon compounds through photosynthesis. Secondary productivity results when heterotrophic organisms consume plant tissues and convert some proportion of that matter and energy to their own biomass.

Energy that is consumed during the business of living is reflected in the release of carbon dioxide from organisms to the environment (i.e. respiration) and the accumulation of matter and energy that we see as biomass increment is only a portion of that actually fixed in photosynthesis, which is called Net Primary Productivity (NPP) while NPP plus respiration is termed as gross primary productivity. NPP is traditionally measured as dry mass. The living biomass present on a site at any given time is called the standing crop.



Total dry matter yield of crop plants results from accumulation of net CO₂ assimilation throughout the growing season. Because CO₂ assimilation results from solar energy absorption and because solar radiation, on a seasonal basis is distributed uniformly over a land surface, the primary factor affecting dry matter yield are the solar radiation absorbed and efficiency of photosynthesis.



For a crop to use solar radiation efficiently most of radiation must be absorbed by green, photosynthetic tissues i.e. leaves. In annual the initial leaf area develops from seedling and is small for much of the early growth, this result in absorption of most of the solar radiation by the soil surface. Many agronomic practices such as starter fertilizer, high plant densities and uniform plant population are used to increase initial ground cover (ground area shaded by leaves) and increase light interception.

Leaf area index (LAI) : Leaf area index expresses the ratio of leaf surface (one side only) to the ground area occupied by the plant.

$$\text{LAI} = \text{Leaf area} / \text{Ground area}$$

A LAI of 1 indicate one unit of leaf surface area per unit of land surface, theoretically could intercept all incident light, but it seldom does, due to leaf shape, leaf angle and leaf distribution. Thus a LAI of 3-5 is usually necessary for maximum dry matter production of most cultivated crops.

Optimum leaf area index: LAI at which maximum CGR (crop growth rate) achieved is considered as optimum LAI for the crop. After which increase in leaf area results in decrease CGR due to shading of lower leaves.

Leaf angle: It is the angle between leaf petiole and stem/branch axis. These angles ranged from planophile to erectophile arrangement. The leaf angle affects radiation interception and light distribution in the canopy.

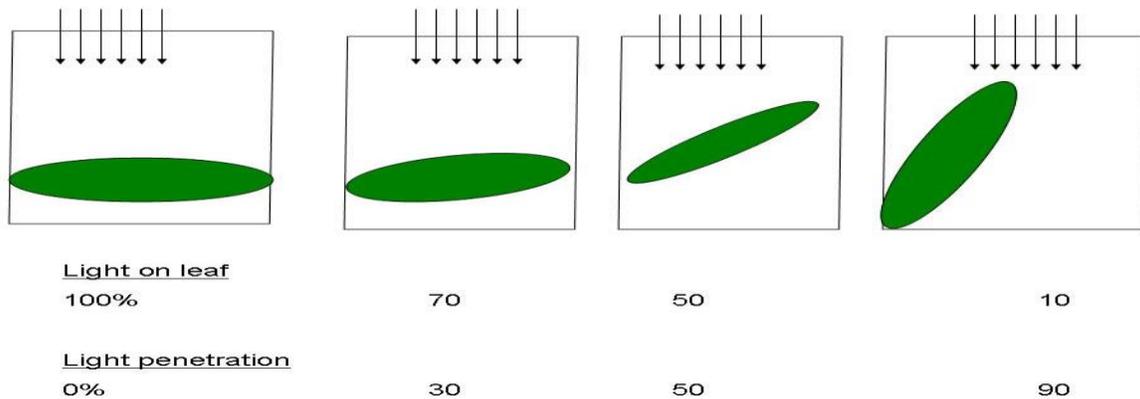


Fig.: Effect of leaf inclination on solar light distribution

Planophile: When leaf angle is less than 35° from horizontal, the leaf inclination termed as planophile. In this case most of leaves are nearly horizontal.

Erectophile: When leaf angle is greater than 60° from horizontal, the inclination pattern termed as erectophile.

Strategies for maximizing solar energy utilization:

Yield is the accumulation of dry matter over time. How efficiently the crop utilizes solar radiation and how long it can maintain utilization results in the final yield of the crop.

Leaf area duration: Leaf area duration expresses the magnitude and the persistence of photosynthetic active leaf area or leafiness during the period of crop growth. Usually the leaf area duration is closely correlated with yield because interception of solar radiation over longer periods of time generally means greater total dry matter production. In theory, the longer the growing period of any crop, higher the total dry matter production and more fruits/seeds plant can produce.

Planting density and Plant distribution:

Efficient interception of solar energy incident to the crop surface requires adequate leaf area, uniformly distributed to give complete ground cover. This is achievable by manipulating planting density (number of plants per unit area of land) and its distribution over the land surface.

Selection of the most suitable planting density must be based on the following factors:

1. Plant size: It reflects leaf area per plant. The leaf area per plant determines the number of plants needed to develop an optimum LAI.
2. Branching : plant density must be planned according to branching habit of the plant.
3. Logging: Increased planting density causes plants and stems to become smaller, weaker and often taller. Thus density must be considered lodging resistance or susceptible nature of the crop.

4. Reduction in fruit set: As density increases, potential flowers and fruits do not set or are aborted. This reduces the final yield.

Maximization of Solar radiation use and crop yield:

1. Planting early for earlier leaf area development.
2. Planting at a seeding rate that will develop an optimal LAI at the maximum leaf area development stage.
3. Planting at a time that provides total ground cover during the period of maximum solar radiation levels.
4. Planting plants uniformly over the land to reduce interplant competition and increase the rate of solar radiation interception.
5. Timely application of fertilization to increase the rate of growth and photosynthetic efficiency of leaf surface.
6. Extending the time of maximum radiation interception by active leaf surface.

Plant Growth Substances/Hormones

Growth of the plant has for long been believed to be due to the minerals absorbed from the soil and the food materials synthesized by the plant. It is now however recognized that the growth of the plant is very much regulated by certain chemical substances known as growth regulators. These substances are formed in one tissue or organ of the plant and are then transported to other sites where they produce specific effects on growth and development.

Plant hormones - They are defined as:

- a. Small
- b. Organic compounds;
- c. Synthesized by the plant;
- d. Active in low concentration
- e. Promote or inhibit growth and developmental responses;
- f. Often show a separation of the site of production and the site of action.

A plant hormone is defined as “**organic substance produced naturally in the higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in minute amounts.**”

There are five major groups, based on chemical structure these groups are: (1) auxins; (2) gibberellins; (3) cytokinins; (4) abscisic acid; and (5) ethylene.

Plant growth regulators: Plant growth regulator term used to describe both naturally and synthetic growth compounds which regulate i.e. promote or retard plant growth.

Plant hormones differ from animal hormones in that:

- No evidence that the fundamental actions of plant and animal hormones are the same.
- Unlike animal hormones, plant hormones are not made in tissues specialized for hormone production. (e.g., sex hormones made in the gonads, human growth hormone - pituitary gland)
- Unlike animal hormones, plant hormones do not have definite target areas (e.g., auxins can stimulate adventitious root development in a cut shoot, or shoot elongation or apical dominance, or differentiation of vascular tissue, etc.).

General Mechanism of hormone action

Hormones act on target tissues to activate a receptor. The general mechanism is:

Hormone-> target tissue/cell -> receptor -> signal amplification -> response

Thus, for a response to occur:

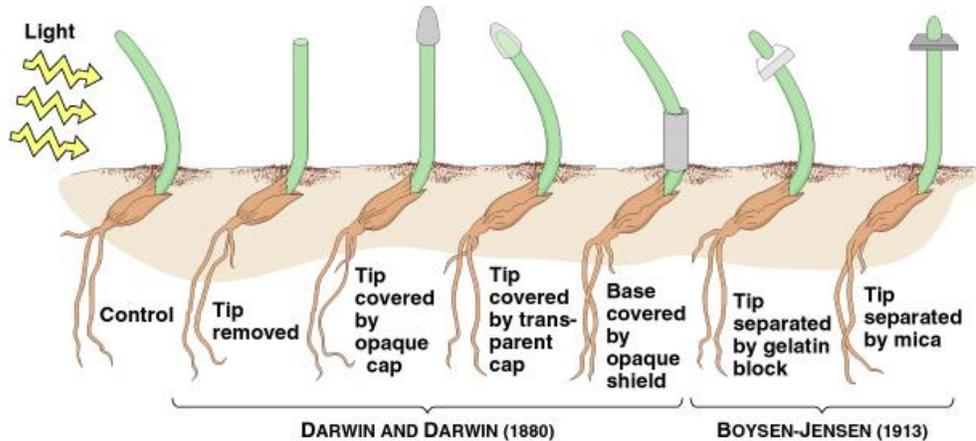
1. the hormone must be present in sufficient quantity;
2. the target tissue must be sensitive to the hormone;
3. the target tissue recognizes the hormone (i.e., there must be a receptor to which the hormone can bind);

4. the binding of the hormone/receptor should initiate a change in the receptor (amplification) and
5. the activated receptor initiates a physiological response

Auxin:

Auxin is a general name for a group of hormones that are involved with growth responses (i.e., elongate cells, stimulate cell division in callus). Not surprisingly, the term "auxin" is derived from the Greek word "to increase or grow". This was the first group of plant hormones discovered.

Darwin (1880) demonstrated that apical tip of seedling (canary grass) are sensitive to unilateral light and show bending towards the light. Similarly, Boysen-Jensen (1913) found that if the mica plate is inserted on the tip, bending is prevented but when gelatin is used bending is observed. These experiments demonstrate the materialistic nature of the substance.



Later on, F.W. Went (1928) isolated the growth substance. He placed several cut *Avena* coleoptile tips on agar block and it was cut into pieces. He placed the agar block piece eccentrically on the coleoptiles cut portion. The growth bending occurred and coleoptile bent on one side opposite to the agar block piece. It occurred due to auxin diffused from agar block to coleoptile resulting into the elongation and growth on that side and as a result coleoptile bends. This method or the bioassay is famous by the name of ***Avena* Curvature Test**.

Chemistry/Structure

A. Naturally Occurring Auxins

The most important auxin found in plants is indole-3-acetic acid (IAA). Other auxins that have been isolated from plants include indole ethanol, indole acetaldehyde, indole acetonitrile, phenylacetic acid (PAA), and 4-chloro-indoleacetic acid. These are probably converted to IAA *in vivo*.

B. Synthetic Auxin

There are a variety of substances that are not known to occur in plants that have auxin activity. These include Indole butyric acid (IBA); Naphthalene Acetic Acid (NAA); 2,4-dichloro-phenoxyacetic acid (2,4-D), and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T).

Biosynthesis

A. Site

Auxin is made in actively growing tissue which includes young leaves, fruits, and especially the shoot apex. Since auxin is synthesized in growing tips or meristematic regions of the plant from where it is transported to other plant parts, the highest concentrations of the auxin are found in these parts such as growing shoot and root tips, young leaves and developing axillary shoots.

B. Pathway

Tryptophan is the precursor of IAA. There can be three different pathways for the biosynthesis of IAA in plants.

1. Indole pyruvic acid pathway

Tryptophan → Indolepyruvic acid → Indoleacetaldehyde → IAA

2. Tryptamine pathway

Tryptophan → Tryptamine → Indole acetaldehyde → IAA

3. Indoleacetonitrile pathway

Tryptophan → Indoleacetaldoxime → Glucobrassicin →
Indoleacetonitrile → IAA

IV. Transport

Auxin is transported in a basipetal (towards the base, base-seeking) direction (Polar transport). In other words, auxin moves from the shoot tip towards the roots and from the root tip towards the shoot.

V. AUXIN RESPONSES:

IAA is involved in the following responses:

A. Cell expansion

Cell expansion is driven by water uptake which in turn results due to relaxation of cell wall pressure. Cell responds to auxin by making cell wall more extensible.

B. Cell differentiation

Promotes differentiation of vascular tissue. (i.e., xylem & phloem).

C. Ethylene production

IAA apparently stimulates the production of ethylene.

D. Inhibition of root growth

[IAA] $> 10^{-6}$ M inhibit root elongation. However, very low ($>10^{-8}$ M) favor root elongation.

E. Cell Division

Auxin has been found to be responsible for initiating and promoting cell division in certain tissues eg. Cambium. Whenever wound is caused in the plant a swelling called callus is developed because of the proliferation of the parenchyma cells stimulated by auxin and a chemical substance traumatic acid. This can be put to practical use in **grafting** where the callus plays an important role in strengthening the union between stock and sion. Hence, during grafting of grapes, it was found that immersion of stock and sion IAA resulted in quick growth of callus and success of graft union.

F. Stimulate root initiation (lateral roots, adventitious roots)

In contrast to the stem, the higher concentration of auxin inhibits the elongation of root but the number of lateral branch roots is considerably increased i.e., the higher conc. of auxin initiates more lateral branch roots. Application of **IAA** in lanolin paste to the cut end of a young stem resulted in an early and extensive rooting. This fact is of great practical importance and has been widely utilized to promote root formation in economically useful plants which are propagated by cuttings.

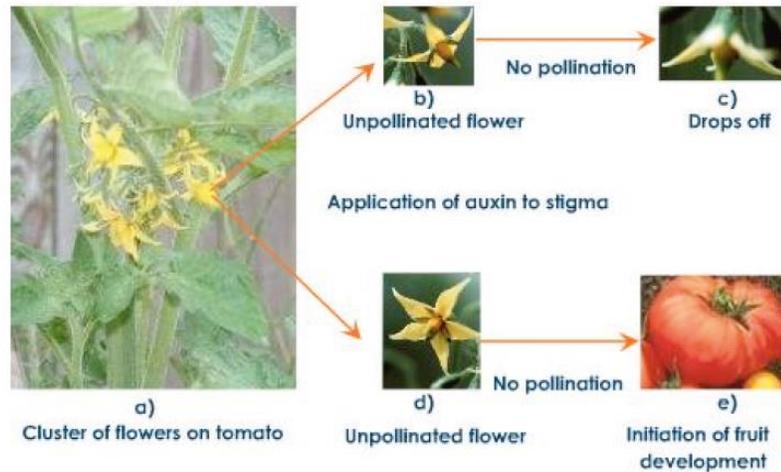
G. Flowering

Although most plants don't initiate the production of flowers after auxin treatment, pineapple and its relatives (Bromeliaceae) do. Once flowers are initiated, in many species, IAA promotes the formation of female flowers, especially in cucurbits (gourd family).

G. Parthenocarpic fruit development

Auxin used in the development of parthenocarpic fruit (formation of fruits without fertilization). As pollen grain is rich source of auxin, pollination trigger fruit growth and by application of auxin, we trigger fruit development without pollination and fertilization to obtain parthenocarpic fruit.

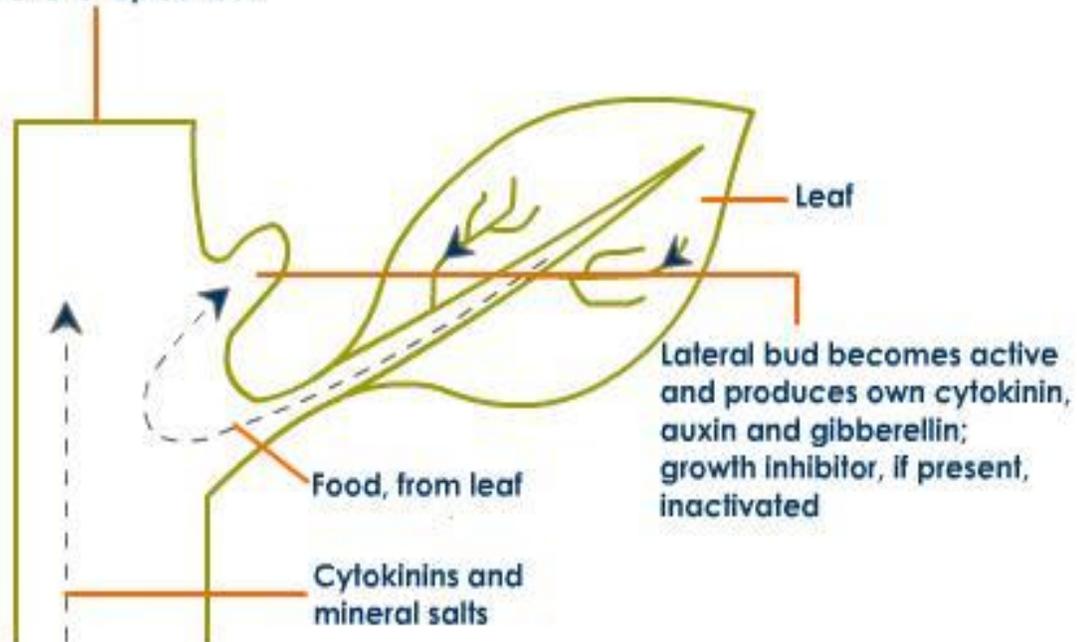
It is a general observation that in the absence of pollination and fertilization the ovary of the flower does not develop into the fruit, but the flower abscises and falls. However application of auxin causes development of ovary into the fruit in several plants such as tomato, brinjal and others. Such fruits are seedless as these have developed without the normal process of fertilization these are known as parthenocarpic fruits. The presence of large number of seeds in a fruit lowers its commercial value in the canning industry.



H. Apical dominance

All shoot tips end in an apical bud, the division of which results in the growth of the stem. It has been a common observation in many vascular plants especially the tall and sparsely branched ones that if the terminal bud is intact and growing, the growth of the lateral buds just below it remained suppressed. This phenomenon of inhibition of laterals by the shoot apex is termed as apical dominance. If the apical bud is removed, the lateral buds show growth. On application of IAA to the cut ends, the lateral buds are again inhibited. So, auxins cause apical dominance. Due to the synthesis of auxin at apical bud, it act as a major sink for cytokinin and other nutrients which limit the supply of these substances to the lateral bud, so lateral buds growth is restricted.

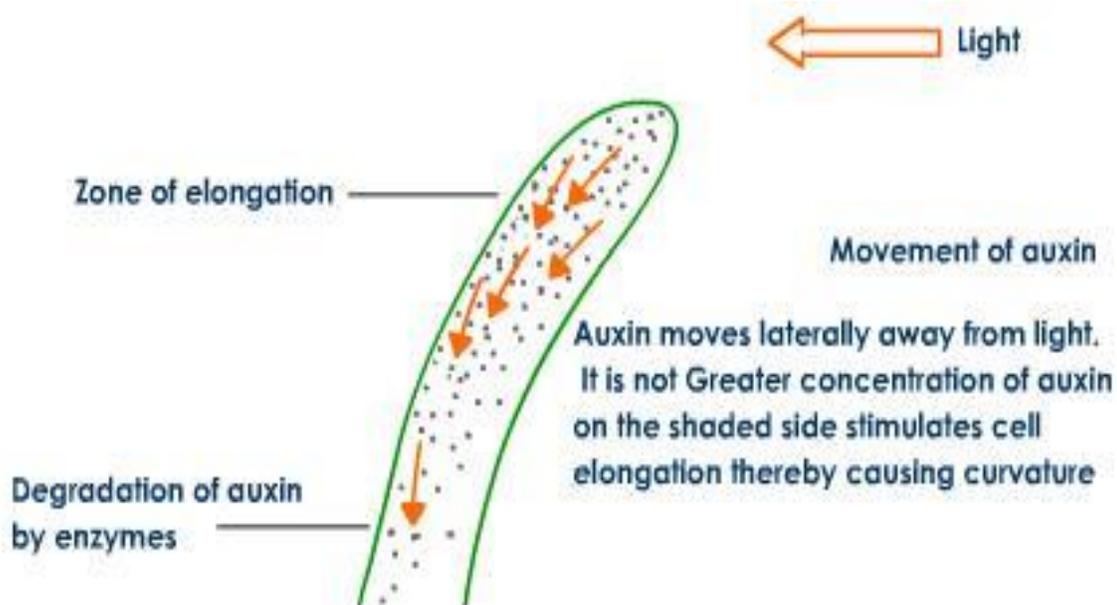
Removal of apical bud



In plants like potato and tomato apical dominance is weak consequently the apical growing point of the main stem fails to suppress the emergence of lateral buds. Such plants are therefore extensively branched and bushy.

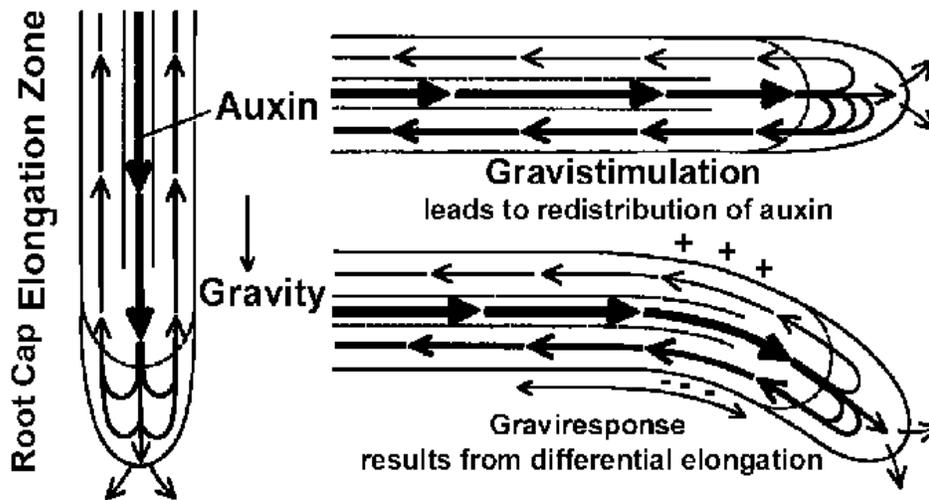
I. Tropisms:

Tropisms are defined as directional response of a plant organ to a directed stimulus in the environment. Auxin has been implied as the major signal for tropic movement. In phototropism auxin in higher concentration accumulated at dark side and causing more growth as compared to illuminated side. Thus due to unequal growth of the two sides, causes bending of the stem towards light. This is known as phototropism.



Hypothesis for effect of unilateral illumination on distribution of auxin in a coleoptile

Similarly, differential growth during gravitropism is based on auxin redistribution. IAA synthesized in the shoot and transported to the root in the stele. When the root is vertical, auxin is distributed equally on all sides of the root. In horizontal root, higher auxin transported to the lower side of the root. The high concentration of auxin on the lower side of the root inhibits growth on that side, while lower concentration at upper side stimulates growth. As a result, the root bends downwards.



J. Abscission

Formation of the abscission layer is correlated with the IAA in leaf. As long as the IAA in the leaf is high relative to the stem, then the abscission layer doesn't form. When the [IAA] in the leaf drops, which occurs normally during the maturity, it stimulates the formation of the abscission layer and the leaf falls.

K. Vascular Differentiation

Auxin induces **vascular differentiation** in plants. This has been confirmed in tissue culture experiments and from studies with transgenic plants. Cytokinins are also known to participate in differentiation of vascular tissues and it is believed that vascular differentiation in plants is probably under the control of both auxin and cytokinins.

Commercial Application:

- Propagation of plant by auxin treatment of cutting scions
- Prevention of pre harvest drop of fruits
- Increase parthenocarpy
- Prevention of sprouting by inhibition of buds
- Increase fruit sets
- Weedicides
- Flowering in pineapple

Characteristics of Auxins:

- Polar translocation
- Apical bud dominance
- Variable behavior of root and shoot growth
- Root initiation
- Delay in abscission
- Differentiation of xylem elements

GIBBERELLINS

I. General

The discovery of Gibberellins was quite accidental. Japanese worker Kurosawa (1926) in Japan while conducting experiments on rice disease caused by *Gibberella fujikuroi* (*causal organism for foolish seedling of rice or bakane disease*) observed that the fungus caused excessive growth in rice. He applied the fungal extracts to intact healthy plants and observed enhanced growth. Later Yabuta and Sumuki (1938) named the active principle as gibberellin. Further it was purified, crystallized and named as gibberellic acid. Now gibberellins are designated as GA₁, GA₂ and so on. The common gibberellic acid is GA₃. At present 112 types of gibberellins are known. Gibberellins are known from angiosperms, gymnosperms, ferns, mosses, algae, fungi and even a few bacteria.

II. Chemistry

- Diterpenes, characterized by having a complex system of 4-5 rings (ent-kaurene ring system) and a carboxyl (acidic) side chain
- More than 110 different gibberellins are known - abbreviated GA₁...GA_n.
- Only a few (about 15) of the GA's have biological activity; the rest are likely breakdown products of, or precursors to, the active ones
- The common gibberellic acid is GA₃ and was the first one discovered and is readily available commercially (produced by *G. fujikuroi* cultures).

III. Biosynthesis

A. Site - young leaves, roots, and developing seeds (developing endosperm) and fruits.

B. Pathway

- terpene pathway
- basic terpene building block is isoprene (isopentenylpyrophosphate, IPP), a five carbon unit
- Five major steps of GA biosynthesis:
 - (1) Synthesis of IPP;
 - (2) Condensation of 4 isoprene units to form geranyl geranyl pyrophosphate (GGPP);
 - (3) GGPP cyclizes to form the kaurene ring system;
 - (4) A methyl group of kaurene is oxidized to a carboxyl group to form GA₁₂-aldehyde;
 - (5) GA₁₂-aldehyde is the precursor to the other GA's

C. GA synthesis inhibitors

- Phosphon D, CCC (cycocel), and Amo1618.
- Ancymidol (A-rest) and paclobutrazol
- Another inhibitor is B-Nine (alar).

Transport

- Made in the tissue in which it is used

- Transport occurs through xylem, phloem, or cell-to-cell.
- Phloem seems to be most important transport route
- Transport is not polar, as it is for auxin.

Actions

A. Promotes stem elongation

Most pronounced effect of gibberellins on the plant growth is the elongation of the internodes, so in plants such as dwarf pea, dwarf maize etc., they overcome the **genetic dwarfism**. For instance, the light grown dwarf pea plants have short internodes and expanded leaves. But, when treated with gibberellin the internodes elongate markedly and they look like tall plants.

B. Seed Germination

Certain light sensitive seeds e.g. lettuce and tobacco show poor germination in dark. Germination starts vigorously if these seeds are exposed to light or red light. This requirement of light is overcome if the seeds are treated with gibberellic acid in dark.

C. Overcomes dormancy in seeds and buds

In temperate regions the buds formed in autumn remain dormant until next spring due to severe colds. This dormancy of buds can be broken by gibberellins treatment. In potatoes also, there is a dormant period after harvest, but the application of gibberellin sprouts the eyes vigorously.

D. Flowering

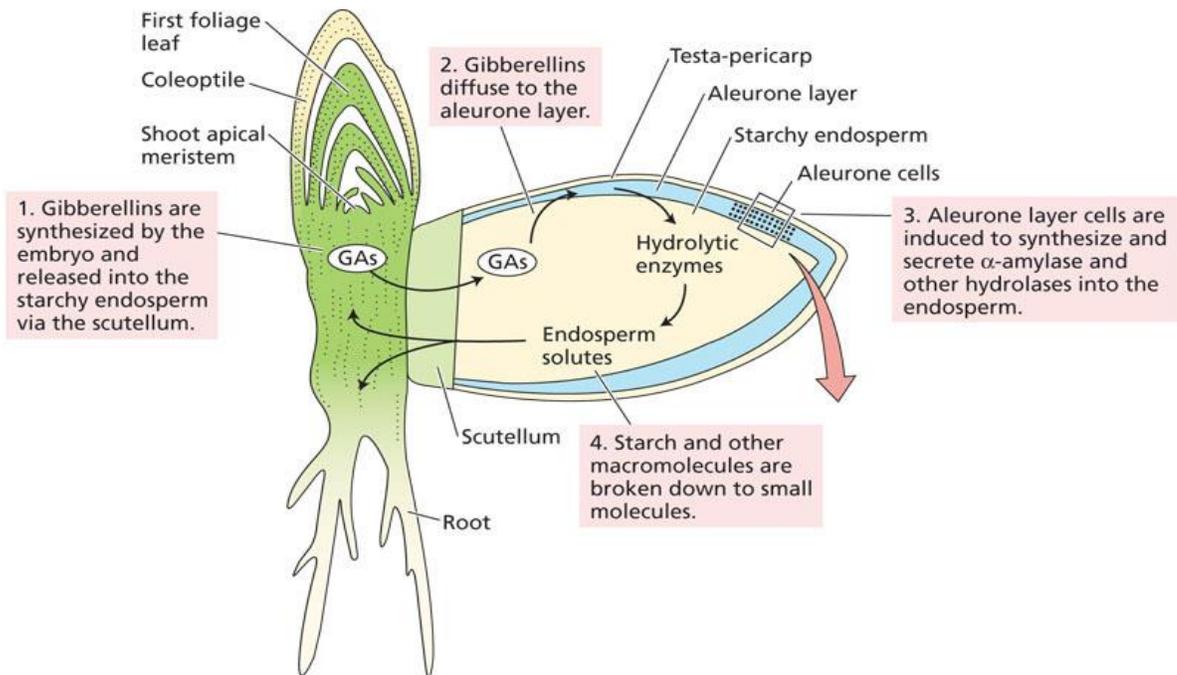
GA stimulates bolting in Long Day plants and can substitute for long days or cold treatments that are necessary for flowering.

In many herbaceous plants the early period of growth show rosette-habit with short stem and cauline leaves. Under short days the rosette habit is retained while under long days bolting occurs i.e., the stem elongates rapidly and is converted into floral axis bearing flower primordia. Production of floral axis is called bolting. Bolting and flowering are induced normally after photo induction or vernalisation. Bolting however can be induced without vernalisation by the treatment of the plant with gibberellins. Many plants require a period of low temperature for flowering. Application of GA replaces the vernalization requirement for the flowering of carrot, beetroot, chicory and others. Vernalization or low temperature requirement is usually met with when the plants pass through natural winter. However this low temperature requirement can be completely overcome and plants can be made to flower in high temperatures by applying GA. Therefore low temperature requirement of plants can be replaced with GA.

E. Mobilization of food reserves in grass seed germination

GA is produced by the scutellum (cotyledon) of the embryo which stimulates the production of amylase by the aleurone layer. Amylase hydrolyzes starch to simple sugars which are absorbed by scutellum and translocated to embryo for growth. Brewers take advantage

of GA's ability to stimulate germination and enzymes which are important in the brewing process.



F. Sex expression

In plants with separate male and female flowers, GA application can determine sex. For example, in cucumber, hemp and spinach, GA treatment increases the proportion of male flowers. In maize, GA treatment causes female flower development.

G. Root Growth

Gibberellins have little or no effect on root growth. At higher concentration in some plants, however, some inhibition of root growth may occur. The initiation of roots is markedly inhibited by gibberellins in isolated cuttings.

Commercial Applications

- Increase size of grapes (spray at time of blooming and fruit set stage)
- Increase distance between grapes in a cluster to minimize fungi/disease
- Breweries - increase starch digestion for malting process
- Delay senescence - spray on fruit like naval oranges
- Sugar cane – increased growth and yields

Cytokinins

I. General

- Called "cytokinins" because they stimulate cell division (*i.e.*, cytokinesis)
- Miller (1956) identified the first cytokinin, called kinetin, in the herring sperm.
- Cytokinins occur in most plants including mosses, ferns, conifers, algae and diatoms

II. Chemistry

A. General

- Adenine derivatives (amino purines)
- Zeatin (Z), which was first isolated from maize (*Zea mays*) is the most common cytokinin.
- Other naturally occurring cytokinins include dihydrozeatin (DHZ) and isopentenyladenosine (IPA).

B. Synthetic cytokinins

- kinetin (*as above*) – probably byproduct of zeatin degradation
- There are several other substances with cytokinin activity such as benzyl adenine (benzylaminopurine; BAP), Thidiazuron

III. Synthesis

Site: synthesized primarily in the meristematic region of the roots. This is known in part because roots can be cultured (grown in artificial medium in a flask) without added cytokinin, but stem cells cannot.

- Cytokinins are also produced in developing embryos.
- First major precursor to the cytokinin is AMP (adenosine monophosphate)

IV. Transport

- via xylem (transpiration stream)
- zeatin ribosides are the main transport form; converted to the free base or glucosides in the leaves

V. Physiological Actions

A. Control morphogenesis

- In plant tissue cultures, cytokinin is required for the growth of a callus (an undifferentiated, tumor-like mass of cells):

callus + auxin + no cytokinin \longrightarrow little growth of callus

callus + auxin + cytokinin \longrightarrow callus grows well, undifferentiated

- Ratio of cytokinin and auxin are important in determining the fate of the callus:

callus + low [cytokinin/auxin] \longrightarrow callus grows well, forms roots

callus + high [cytokinin/auxin] \longrightarrow callus grows well, forms meristem & shoots

B. Cell division

Regulates the cell cycle/cell division (hence, the name "cytokinins) – especially by controlling the transition from G2 → mitosis.

C. Cytokinin levels delay senescence: Anti Senescence hormone (Richmond - Lang effect)

The ageing process of the leaves usually accompanies with loss of chlorophyll and rapid breakdown of proteins. This is called senescence.

Cytokinin application to an intact leaf markedly reduces the extent and rate of chlorophyll and protein degradation and leaf drop. The delay of senescence of leaves and other organs of the plants by cytokinins is called as **Richmond - Lang effect**.

For example, as detached leaves senesce the cytokinin levels drop. And, when these leaves are treated with auxin to stimulate rooting, when roots form the senescence process stops and cytokinin levels rise. This delay in senescence due to application of cytokinin also termed as Richmond Lang effect.

D. Promote lateral bud development (Overcome apical dominance):

Cytokinin application to dormant buds will cause them to develop. These results suggest that apical dominance may be related to cytokinin, too.

E. Dormancy of seeds

Like gibberellins, the dormancy of certain light sensitive seeds such as lettuce and tobacco can also be broken by kinetin treatment in dark. The inhibitory effect of far red light treatment on the germination of the above seeds is also overcome by kinetin treatment.

Commercial application:

1. Increasing shelf life of fruits
2. Quickening of root induction and production of efficient root system
3. Breaking dormancy
4. Increasing yield and oil content in groundnut.

Abscisic Acid (ABA)**I. General**

- Addicott (1965) found a substance that stimulated abscission of fruits in cotton and they named it abscisin II
- About the same time, Wareing found a substance in sycamore leaves that promoted dormancy in buds and called it dormin
- It was soon clear that these were the same substance and a conference in 1967 straightened out the name and it was decided to call the hormone abscisic acid (ABA).

II. Chemistry

- A single structure, not a family of related structures like the gibberellins
- It is a sesquiterpene (*i.e.*, terpenoid) (C₁₅) - made from 3 isoprene units
- Found in all green plants, also in some mosses, algae, and fungi
- Related to lunularic acid which is found in liverworts.

III. Biosynthesis

- Synthesized in plastids
- most tissues, especially leaves and seeds
- ABA derived from the breakdown of carotenoids.

IV. Transport - xylem and phloem (greater amounts)

V. Actions

A. Growth Inhibitor

Widespread growth inhibitor; often antagonistic of GA actions

B. Maintains or "seals in" bud and seed dormancy (i.e., prevents germination)

In fact, ABA is made during the terminal stages of embryo development. Among its roles in seed dormancy is to: (1) provide desiccation tolerance of the embryo by promoting synthesis of proteins involved in the process; and (b) promote accumulation of seed storage proteins.

Seeds of apple remain dormant and fail to germinate till they are exposed to a period of stratification. Such seeds show the presence of ABA. When the seeds are stratified the ABA content falls with a corresponding increase in GA content. Thus, it can be concluded that the seed dormancy is controlled by GA-ABA balance at least in some species.

ABA helps in inhibiting precocious germination and vivipary. This is very important because dormancy caused by ABA does not allow the seed to germinate while it is still on its mother plant.

In woody species, dormancy is an important adaptive feature in cold climates. When a tree is exposed to very low temperatures in winter it protects its meristems with bud scales and temporarily stops bud growth.

C. Stress hormone: A very different role of ABA has been reported in plants growing under stress environment such as drought, flooding, injury etc. A fairly high concentration of ABA is found in leaves of such plants. During water stress ABA induces stomatal closure.

D. ABA inhibits GA stimulated growth in various forms. Therefore ABA is known as antigibberellin.

E. Stomatal regulation

The role of ABA in causing stomatal closure in plants undergoing water-stress is well known. As water stress begins, root cells synthesize ABA and transport it to leaves via xylem stream. In response to the water-stress, the permeability of the guard cells to ABA is greatly increased as compared to mesophyll cells. However, when the water potential of the plant is restored (*i.e.*, increased), the movement of ABA into the guard cells is arrested. The application of exogenous ABA causes closing of stomata by inhibiting the ATP-mediated H⁺/K⁺ ion exchange pumps in guard cells.

Ethylene (Ripening hormone)

I. General

- The Chinese may have been the first to observe the effects of ethylene when they noted that burning incense increased fruit ripening
- In 1864 leaks in gas lights in street lamps were reported to stunt plant growth and defoliate trees
- In 1901, D. Neljubow realized that his dark-grown pea seedlings were short, fat and negatively gravitropic (the triple response) because of a component in "laboratory air" which he subsequently identified as ethylene
- Cousins (1910) first reported that ethylene occurred in plants. Gane (1934) clearly established that ethylene is actually a natural product of ripening fruits and is responsible for hastening ripening process.

II. Chemistry

- single compound and is not a family of related ones
- $\text{CH}_2=\text{CH}_2$
- ethylene (MW 28) is similar in size/shape as water
- A gaseous plant hormone

III. Biosynthesis

A. General:

- made by most plants including angiosperms, gymnosperms, ferns, mosses, liverworts
- also synthesized by fungi and bacteria
- made by all parts of the plant
- meristematic regions (shoot apex) and senescing tissues are rich sources
- nodes make more ethylene than internodes
- ethylene production is stimulated by physiological stresses including wounding, anaerobic conditions, flooding, chilling, disease and drought.
- during the climacteric – which is the sudden surge of respiratory activity that occurs at the peak of ripening in many fruits - lots of ethylene is made

B. Pathway of synthesis

- The first precursor is methionine (one of the protein amino acids)
- Methionine + ATP \rightarrow S-adenosyl-methionine (SAM) \rightarrow ACC synthase \rightarrow amino cyclopropane carboxylic acid (ACC) \rightarrow ACC oxidase \rightarrow $\text{CH}_2=\text{CH}_2$
- Ethylene biosynthesis exhibit autocatalytic effect i.e as synthesis starts it increases more additional ethylene synthesis itself.

IV. Inhibitors

- Silver ions (Ag^+), CO_2 and KMnO_4 inhibit ethylene actions. These bind to ethylene receptors or otherwise interfere with the mechanism of ethylene action.
- Aminovinylglycine (AVG) and aminoxyacetic acid (AOA) block the action of ACC synthase.

- Silver ions (Ag^+) applied as silver nitrate (AgNO_3) or as silver thiosulfate (STS) are potent inhibitors of ethylene action. Silver is very specific; the inhibition it causes cannot be induced by any other metal ion.
- Carbon dioxide at high concentrations (in the range of 5 to 10%) also inhibits many effects of ethylene, such as the induction of fruit ripening, although CO_2 is less efficient than Ag^+ . This effect of CO_2 has often been exploited in the storage of fruits, whose ripening is delayed at elevated CO_2 concentrations.

V.Actions

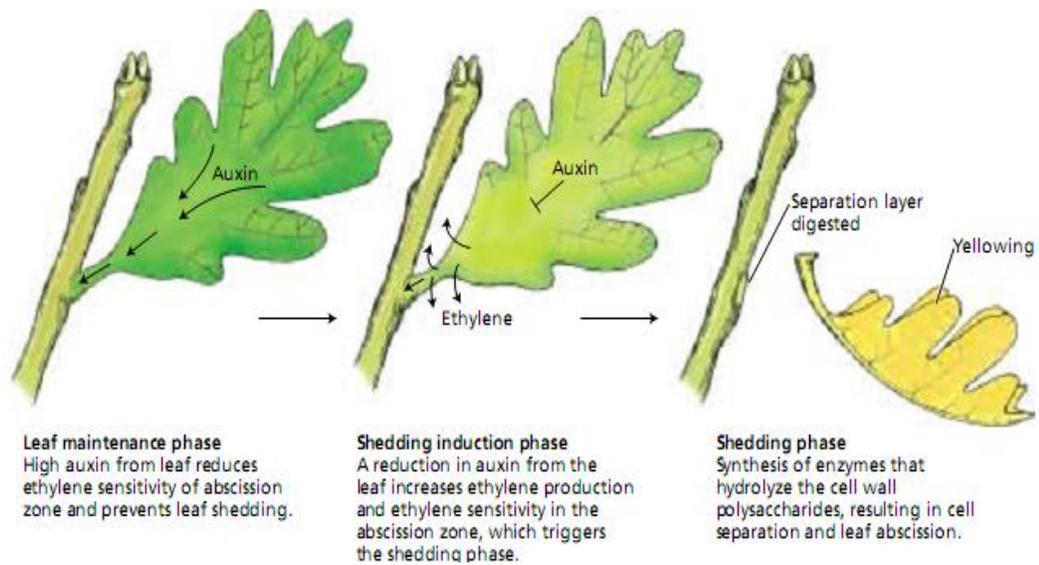
A. Fruit ripening

In everyday usage, the term fruit ripening refers to the changes in fruit that make it ready to eat. Such changes typically include softening due to the enzymatic breakdown of the cell walls, starch hydrolysis, sugar accumulation, and the disappearance of organic acids and phenolic compounds, including tannins. From the perspective of the plant, fruit ripening means that the seeds are ready for dispersal. Ethylene triggers fruit ripening. As fruits mature, ethylene biosynthesis increases. All fruits that ripen in response to ethylene exhibit a characteristic respiratory rise before the ripening phase called a climacteric. Such fruits also show a peak of ethylene production immediately before the respiratory rise. In as much as treatment with ethylene induces the fruit to produce additional ethylene, its action can be described as autocatalytic. Apples, bananas, avocados, and tomatoes are examples of climacteric fruits. In contrast, fruits such as citrus fruits and grapes do not exhibit the respiration and ethylene production rise and are called non climacteric fruits.

Climacteric and nonclimacteric fruits	
Climacteric	Nonclimacteric
Apple	Bell pepper
Avocado	Cherry
Banana	Citrus
Cantaloupe	Grape
Cherimoya	Pineapple
Fig	Snap bean
Mango	Strawberry
Olive	Watermelon
Peach	
Pear	
Persimmon	
Plum	
Tomato	

B. Abscission

This is the shedding of plant parts. It occurs at a specialized layer of cells – the abscission layers. Auxin apparently prevents leaf abscission by maintaining cells in the abscission zone insensitive to ethylene. When at maturity auxin levels in the leaf decline, the tissues become sensitive to ethylene that promotes abscission by producing and secreting cellulases, etc.



C. Epinasty

When the upper side (adaxial side) of the petiole of a leaf grows faster than the lower side (abaxial side), the leaf curves downward. This is called as epinasty. Ethylene causes leaf epinasty in tomato and other dicot plants such as potato, pea and sunflower. Young leaves are more sensitive than the older leaves. However, monocots do not exhibit this response. Higher concentration of auxin, stress conditions such as salt stress, water-logging and pathogen infection also induce leaf epinasty indirectly through increased ethylene formation. In tomato and other plants, water-logging creates anaerobic condition around the roots resulting in accumulation of ACC (1-amino cyclopropane-1-carboxylic acid) (the immediate precursor of ethylene formation) in roots. ACC is then translocated to shoots along with transpiration stream where it is converted into ethylene in presence of oxygen and induces leaf epinasty.

D. Triple Response

Ethylene causes 'triple response' of etiolated seedling such as in pea which consists of (i) inhibition of stem elongation, (ii) stimulation of radial swelling of stems and (iii) horizontal growth of stems with respect to gravity (i.e., diageotropism).

E. Flowering

Ethylene is known to inhibit flowering in plants. However, in pineapple and its allies (Family Bromeliaceae) and also in mango, it induces flowering. Ethylene is used commercially to synchronize flowering and fruit set in pineapple.

F. Sex Expression

In monoecious species (with separate male and female flowers on the same plant) especially **some cucurbits** like, cucumber, pumpkin, squash and melon, ethylene strongly promotes formation of female flowers thereby suppressing the number of male flowers considerably.

G. Senescence

Ethylene enhances senescence of leaves and flowers in plants. During senescence, concentration of endogenous ethylene increase with decrease in concentration of cytokinins and it is now generally held that a balance of these two phytohormones controls senescence. Freshly cut carnation flowers when held in water in a conical flask, loose colour of their petals and wither (*i.e.*, senescence) within a few days. But, if the cut carnations are held in conical flask containing silver thiosulphate solution, they remain fresh for many weeks. This is because silver thiosulphate is potent inhibitor of ethylene action.

Commercial applications

Ethrel (Ethephon) is a commercial formulation of ethylene. It contains a dilute solution of **2-chloro ethyl phosphonic acid** that breaks down to give off ethylene.

1. It is used to synchronize flowering and fruit set in pineapples.
2. Degreening of citrus and banana fruits
3. Fruit thinning and fruit drop in cotton, cherry and walnut

GROWTH RETARDANTS

The term growth retardant refer to the chemicals that slow down cell division and cell elongation of shoot tissue and regulate plant height physiologically without formative effects. They do not occur naturally in plants.

Examples:

- AMO 1618 ,
- CCC (Chloro choline chloride) (2-Chloroethyl – trimethyl ammonium chloride)
- Chlormequat chloride (Cycocel)
- Alar or B9
- paclobutrazol
- Mepiquat chloride

Paclobutrazol

It is widely used to reduces the problem of biennial bearing in Mango. Suppression of growth by paclobutrazol occurs because the compound blocks three steps in the terpenoid pathway for the production of gibberellins by binding with and inhibiting the enzymes that catalyze the metabolic reactions. When gibberellin production is inhibited, cell division still occurs, but the new cells do not elongate. The result is shoots with the same numbers of leaves and internodes compressed into a shorter length.

GROWTH INHIBITORS:

Growth inhibitors suppress the growth of plants. ABA and ethylene are called as natural growth inhibitors. They bring about certain formative changes in plants. There are synthetic growth inhibitors also.

Examples: Malichydrazide (MH), 2,3,5-T, Triiodo benzoic acid (TIBA)

Maleic hydrazide**Role**

- Inhibition of seed germination
- Induction of dwarfing effect.
- Stimulates branching and lateral shoot growth and prevents apical dominance
- Prolonged bud dormancy
- Prevents flowering in short day plants
- Prevents sprouting of onions and potatoes during storage

Mechanisms of Abscission and Senescence of leaves

Abscission of leaves

Detachment of the older (rather senescent) leaves or leaf fall is a common phenomenon in plants and is called as abscission of leaves. Abscission is quite distinctive in deciduous trees and shrubs of temperate regions in autumn when all the leaves of such plants fall at about the same time giving the plants a naked appearance, the new leaves developing in the subsequent spring. In evergreen plants there is gradual abscission of leaves, the older leaves fall while new leaves are developed continuously throughout the year. In most of the herbaceous species, however the leaves are not shed even after they die and in many cases are retained in withered dry condition even after the whole shoot is dead. Leaf abscission takes place at the base of the petiole which is internally marked by a distinct zone of few layers of thin-walled cells arranged transversally across the petiolar base. This zone is called as the abscission zone or abscission layer. The cells of the abscission layer separate from each other due to the dissolution.

Mechanism of abscission

The young leaves remain attached to the stem and do not abscise till they become old. However, if the blade or lamina portion of a young leaf is cut, the debladed petiolar stump soon abscises. In case auxin (IAA) in lanolin paste is applied to the cut end of petiole of such a young leaf the abscission of the petiolar stump is greatly suppressed. The intact young leaf does not abscise because its lamina portion contains auxin synthesized by it. These experiments have led to the belief that auxin has controlling influence in the abscission of leaves. This belief is further strengthened by the fact that endogenous auxin concentration in leaves falls considerably at the time of normal abscission.

Normally, the auxin level of the stem side of the abscission zone is probably maintained due to basipetal transport of auxin from the stem tip while the source of the auxin on the blade side of the abscission zone is the blade or lamina of leaf itself. The above-mentioned experiments have led to the establishment of auxin gradient hypothesis according to which it is not the presence or absence of auxin but relative concentration of auxin on stem side of the abscission zone or nearly equal concentration of auxin on both its sides will promote abscission while higher concentration of auxin on the blade side of the abscission zone will retard abscission.

Besides auxin, other growth hormones especially ethylene may also play important role in abscission. It is now believed that the relative concentration of auxin on two sides of the abscission layer has regulatory influence on the production of ethylene that stimulates leaf abscission. At the time of abscission, concentration of auxin in the laminar region decreases with simultaneous increase in ethylene production. This also increases sensitivity of cells of abscission zone to ethylene which now synthesize cell wall degrading enzymes such as cellulases and pectinases. Activity of these enzymes results in cell wall loosening and cells separation ultimately leading to leaf abscission.

SENESCENCE

The term senescence' is derived from a Latin word "Senescere" which means to grow old'. The terms Senescence, Programmed Cell Death (PCD)' Apoptosis' and Ageing' are often used synonymously in plant or animal systems. All these terms generally refer to death of cells, organs or organisms. In the life cycle of higher plants when they have reached a certain stage of maturity, they senesce and die. It should be clarified that the ageing is not the same as senescence. 'A degenerative and irreversible change in a plant which leads to death' is called **senescence** where as **ageing** is 'the process of attaining maturity with the passage of time'.

PHYSIOLOGICAL AND BIOCHEMICAL CHANGES DURING SENESCENCE:

1. Yellowing of leaves because of decline in chlorophyll content.
2. Decrease in photosynthetic rate. This may be due to
 - a. Ultra structural changes in chloroplasts
 - b. Decrease in chlorophyll content Synthesis
 - c. Increase in stomata resistance and
 - d. Decrease in the activity of Rubisco enzyme
3. Cells undergo reduction of their structure

CLASSIFICATION OF SENESCENCE (TYPES OF SENESCENCE):

Depending upon the part of the plant in senescence, **Leopold** (1961) has classified senescence in to following four categories.

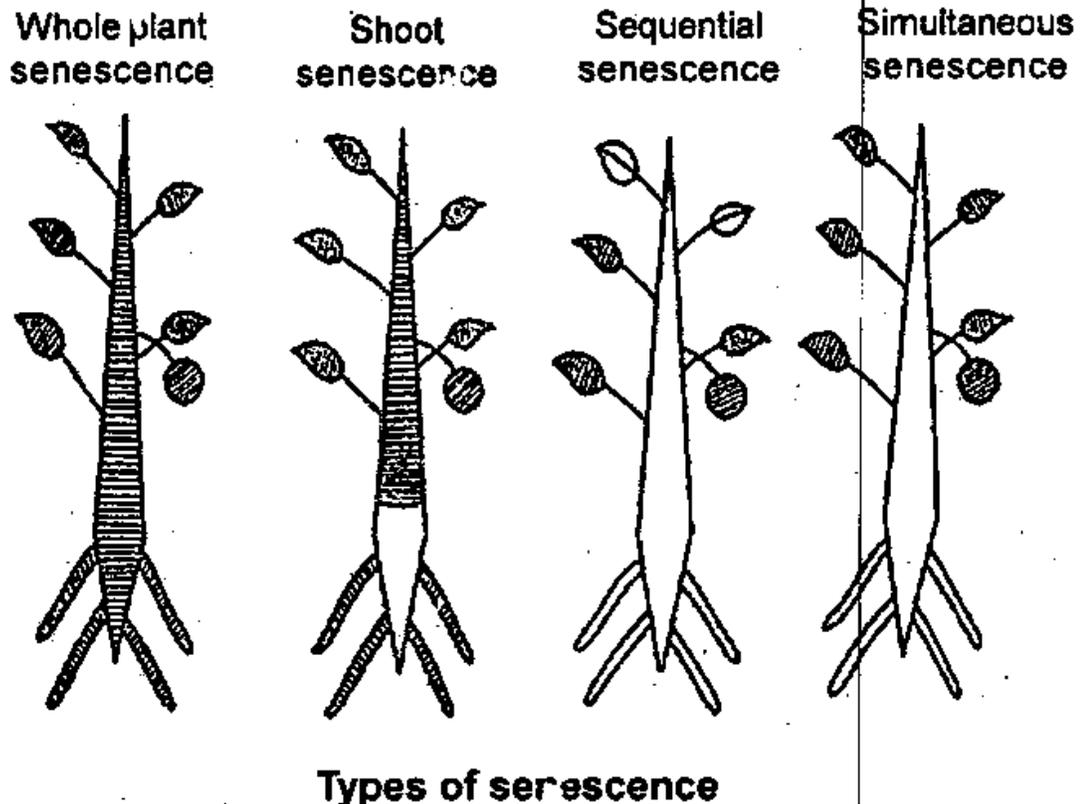
A. **Overall senescence:** (whole plant senescence): In this kind of senescence, there is senescence and death of the entire plant, which usually takes place at the end of reproductive phase. eg: Cereal crops like maize, wheat and rice and also in mustard and cabbage.

B. **Progressive senescence:** In normal development of most annual plants, there is progressive senescence, where the oldest leaves senesce and die first. The senescence moves from leaves to the stem and then to underground parts. eg: Tobacco.

C. **Top senescence** (Shoot senescence): Here senescence and death of all above ground parts occurs, while the underground root portions survive and give rise to new buds in the next season.

eg: Sugar beet, Banana, Ginger

D. **Deciduous senescence** (simultaneous senescence): In this kind of senescence, all leaves senesce and die, leaving the stem and roots alive as in gulmohar (*Delonix regia*) and Raavi (*Ficus religiosa*), Eucalyptus.



The occurrence of senescence differs both in their causes and in its nature. Senescence of the entire plant after a single reproductive cycle is called **monocarpic senescence**. Senescence may be delayed when flowers and fruits are removed. Some monocarpic plants like *Agave americana* generally live and grow for many years before flowering. They die when they produce fruits. Thus senescence is an irreversible one. On the other hand in tobacco plant older leaves senesce as the plant grows.

SIGNIFICANCE OF SENESCENCE:

The main purpose of leaf senescence is to recover the nutrients, specially nitrogen and carbon for the growth of younger leaves and other developing organs on the plant. The senescence of leaves in deciduous trees is also a mechanism of avoiding extreme environmental conditions such as severe cold. Of late scientists are trying to develop “**stay green varieties**” which can retard the process of leaf senescence and can maintain green leaves for a longer period.

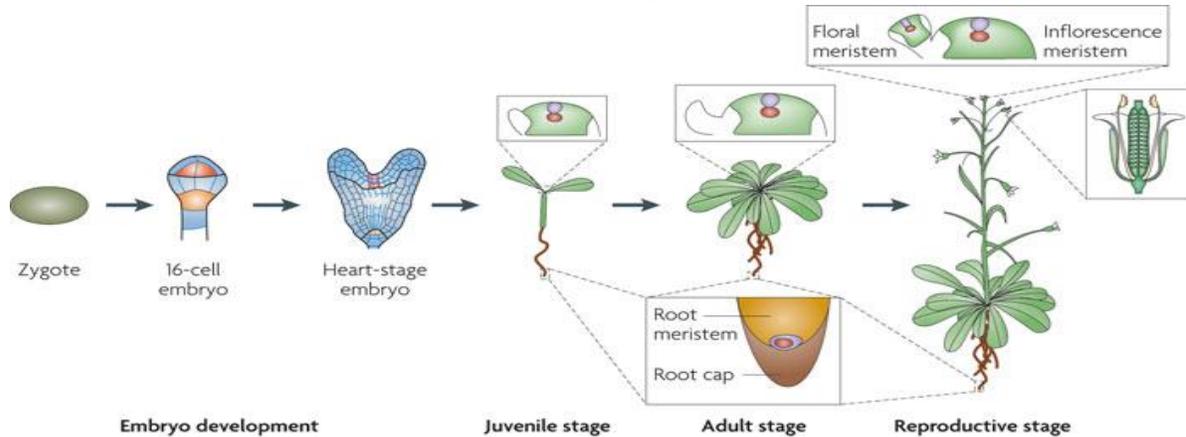
The term *abscission* is used to describe 'the processes involved in the shedding of plant structure, characterized by the degradation of cell walls at the point of weakening'. Cells surrounding the fracture line produce and secrete cell wall degrading enzymes which hydrolyze the central region of the wall allowing the cells to separate for fracture to occur. This fracture occurs in "Separation layer" which is 1-3 cells wide. Plants do not have the ability to produce separation layer anywhere. They are genetically limited to specific locations called "Abscission Zones" which are 5-50 cells wide. Cells of abscission zone are somatic and have more persistent meristematic activity. Lignified structural elements like fibers and sclereids are absent in abscission zone and are replaced by collenchymas. Lignified walls are extremely resistant to enzymatic hydrolysis while collenchymas walls are readily degradable. Abscisic acid was originally isolated as an "abscission causing factor". However it is evident that ABA stimulates abscission of organs in only few species and that the primary hormone causing abscission is ethylene. On the other hand ABA is clearly involved in senescence, and through promotion of senescence it might indirectly increase ethylene formation and stimulate abscission. Senescence acts as a signal for inducing abscission and senescence of plant parts usually precedes the abscission but there are examples where leaf senescence occurs in the autumn and abscission does not occur until the following spring. Thus, the linkage between senescence and abscission can be broken since, both processes occur independently.

REGULATION OF FLOWERING

An overview

The initiation of flower primordia is a major event in the life cycle of a plant in that it involves a shift in the phase of development from vegetative to reproductive. The process of flowering requires the vegetative meristem (buds) to change into a reproductive meristem. This process involves the following sequence of events:

Juvenile vegetative phase → adult vegetative phase → adult reproductive phase
→ flowering



Juveniles vs. adults

Juvenile plants cannot flower; they are capable of only vegetative growth. Thus, like in humans and other animals, the ability to reproduce marks the transition from the juvenile phase to adulthood.

Ripeness to Flower

Before floral primordia can be initiated, the plant must complete a period of vegetative growth or attain some minimal leaf number. When this condition is attained, the plant is said to be ripe to flower. Ripeness-to-flower is not recognized by any external characteristics, but it can be determined empirically by subjecting plants of varying age (From seedling emergence) to environmental conditions known to induce flowering. In most plants ripeness – to- flower is attained after the plant has produced several leaves. The adult can flower and is said to be "***ripeness -to- flower***" or "***competent***". In other words, it has the potential to flower when the conditions are appropriate. This may be a mechanism to insure that there is a sufficient vegetative mass (*i.e.*, leaves, roots) to support the reproductive output.

Juvenile to Adult Transformation:

The maturation of the juvenile into the adult may be mediated by a variety of factors including:

1. size (*more important than age*)
2. age (ex. bamboo);
3. leaf number;

4. growth conditions (conditions that favor growth promote the transition to adult phase; poor conditions, such as water stress, lack of light, low temp, prolong the juvenile phase)

Ultimately, one or more of these factors likely induce changes in (1) hormones (2) nutrient levels (3) other chemicals that in turn trigger the developmental switch to adulthood.

Adult Vegetative-to-Reproductive Transition

The transition from the vegetative to reproductive buds is usually triggered by an environmental signal, typically photoperiod or temperature. This signal synchronizes flowering to environmental events. Thus, this is a type of "timing mechanism" that plants use to coordinate actions with the season. If flowers are produced at the wrong time of the year the pollinator may not be available, or it may be too dry (or wet), or there may not be enough time before winter to allow time for successful seed set. Once the inductive signal has been received then the plant meristem is said to be "determined". In other words, it is now committed to flower.

Thus, we can modify the flowering scheme again

Juvenile vegetative phase → transition factors (i.e., size, age) → induce hormonal or other changes → adult vegetative phase → environmental signal (i.e., photoperiod, temperature) → adult reproductive phase → flowering expressed

Light, or more specifically, photoperiod and flowering

Attainment of the ripe-to-flower condition does not automatically lead to the initiation of flower primordia. Certain environmental conditions must follow. These same environmental conditions, if presented to a plant that is not in ripe to flower condition, will not bring out flowering response. W.W Garner and H. A. Allard (1920) two plant physiologists with the U.S. Department of Agriculture, found that day length, or the duration of light and dark periods within a 24 hour cycle, also influenced the initiation of flowering.

A. A brief history.

Garner's and Allard's classic studies showed that a tobacco mutant variety, Maryland Mammoth, which failed to flower under field conditions, did so in the greenhouse in the winter in response to photoperiod.

B. The flowering response to day length varies with the species:

The plants in order to flower require a certain day length *i.e.*, the relative length of day and night which is called as photoperiod. The response of plants to the photoperiod expressed in the form of flowering is called as **photoperiodism**.

Depending upon the duration of the photoperiod, they classified plants into three categories.

1. Short day plants (SDP) - require one or more days with less than a certain amount of daylight. Or, the critical day length to induce flowering must be less than some maximum. These species usually flower in the spring or fall. Usually these plants require a relatively

short day light period (usually 8-10 hours) and a continuous dark period of about 14-16 hours for subsequent flowering.

Ex: Rice, soybean, sugarcane, chrysanthemum, etc.

2. Long day Plants (LDP) – LDP require one or more days with more than a certain critical day length to flower. The critical day length must be longer than a minimum. These plants require a longer day light period (usually 14-16 hours) in a 24 hours cycle for subsequent flowering.

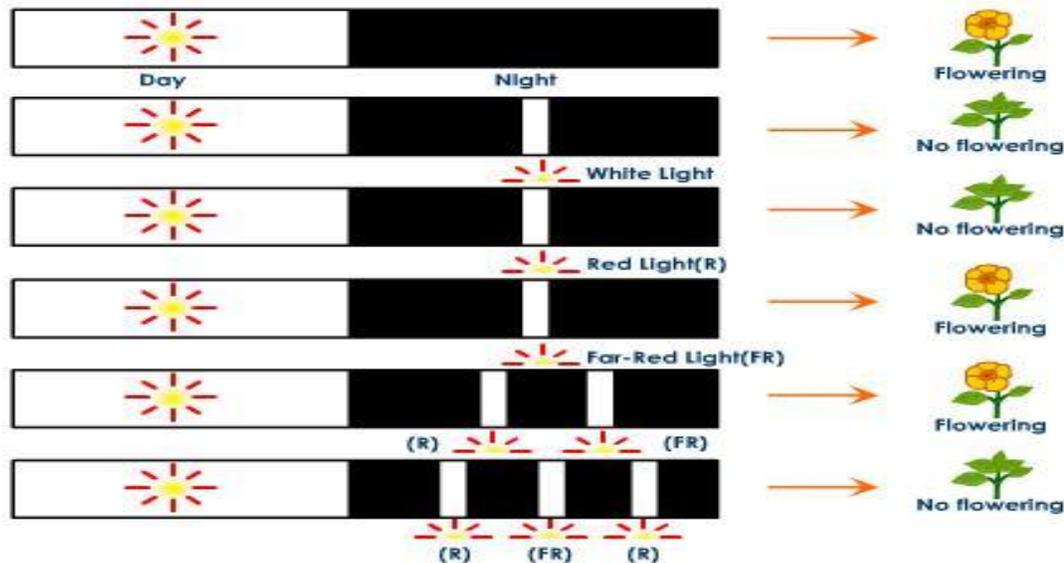
Ex: Wheat, oat, radish, alfalfa etc.

3. Day neutral plants (DNP) – Their flowering is not affected by the length of the day.

Ex: Tomato, cucumbers, maize, pea etc.

C. The night period is more important than the day.

Cocklebur, a SDP, flowers if it received one critical photoperiod with less than 8 hours of light (or, > 16 h darkness). The proportion of light/dark is not important in flowering. A light break during the night interrupts the flowering response, but a dark period during the day has little effect on flowering. The timing of the night break is important. Initial and later interruption has little effect than interruption at middle.



Conclusion: long day plants can be called "short night plants" and short day plants can be called "long night plants".

D. Receptor of photoperiod:

1. Location.

The receptor is located in the leaves.

Evidence: (a) defoliated plants are insensitive to photoperiod;

(b) Plants with a single leaf in the inductive photoperiod will bloom

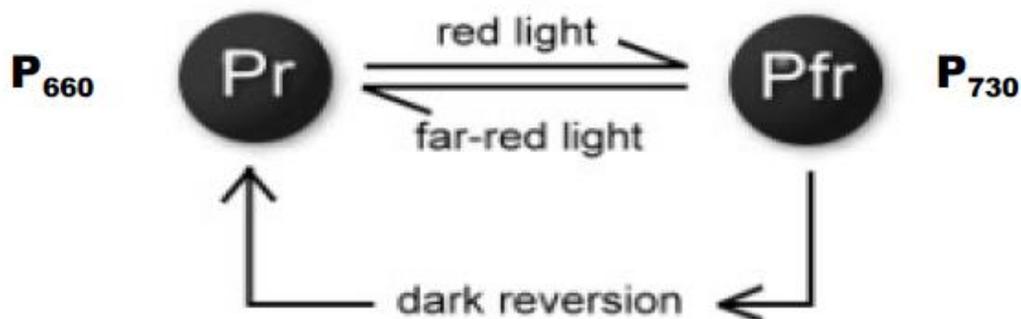
(c) The receptor doesn't seem to reside in meristem since treating the meristem with inductive photoperiod doesn't initiate flowering.

Plants may require one or more **inductive cycles** for flowering. An appropriate photoperiod in 24 hours cycle constitutes one inductive cycle. If a plant which has received sufficient inductive cycles is subsequently placed under unfavorable photoperiods, it will still flower. Flowering will also occur if a plant receives inductive cycles after intervals of unfavorable photoperiods (*i.e.*, discontinuous inductive cycles.) This persistence of photoperiodic after effect is called **photoperiodic induction**.

2. Nature of the receptor.

Since light is involved, it suggests that a pigment plays a role in photoperiodism. Phytochrome is a likely candidate because: (a) the light break shows red/far red sensitivity; (b) the action spectrum for the light break in cocklebur is consistent with phytochrome. In fact, there is evidence for the participation of two forms of phytochrome. It is a chromophore protein. The phytochrome is a soluble protein with a molecular weight of about 250 kDa. It's a homodimer of two identical polypeptides each with a molecular weight of about 125 kDa. Each polypeptide has a prosthetic group called as chromophore which is covalently linked to the polypeptide via a sulphur atom in the cystine residue of the polypeptide. The protein part of the phytochrome is called as apoprotein.

The unique feature of phytochrome is that it exhibits photoreversibility; it exists in two forms that are interchangeable. Pr - red light absorbing form and Pfr - far red light absorbing form. When Pr absorbs red light (*ca.* 660 nm) it is converted into Pfr. When Pfr absorbs far red light (*ca.* 730 nm) it is converted into Pr. In short, phytochrome acts like a light switch. This can be depicted:



Phytochrome and Flowering in Short Day Plants:

At the end of light period the phytochrome is predominantly present in the pfr form and the ratio of Pfr to Pr is such that, the formation of the flowering stimulus is prevented. During the long dark period, spontaneous conversion of Pfr to Pr takes place or Pfr is destroyed, and the ratio of Pfr to Pr finally drops to a level where metabolic processes are triggered which leads to the formation of flowering stimulus. This duration represents the critical dark period requirement for the flowering of SDP. It varies from plant to plant. If the

dark period is interrupted by flash of red light, Pr is converted to Pfr. And the Pfr to Pr level is such that the formation of the flower stimulus is prevented.

Phytochrome and Flowering in Long Day Plants:

Long day plants require a high ratio of Pfr to Pr for the formation of flowering stimulus. Such a high ratio of Pfr to Pr is attained at the end of a long day. If the night is too long, Pfr reverts to Pr or is destroyed and the flowering stimulus is prevented from being formed. When the night is interrupted by a flash of red light, Pr is converted to Pfr, thereby raising the ratio of Pfr to Pr to a level which allows the flower stimulus to form.

Evidence for flowering hormone:

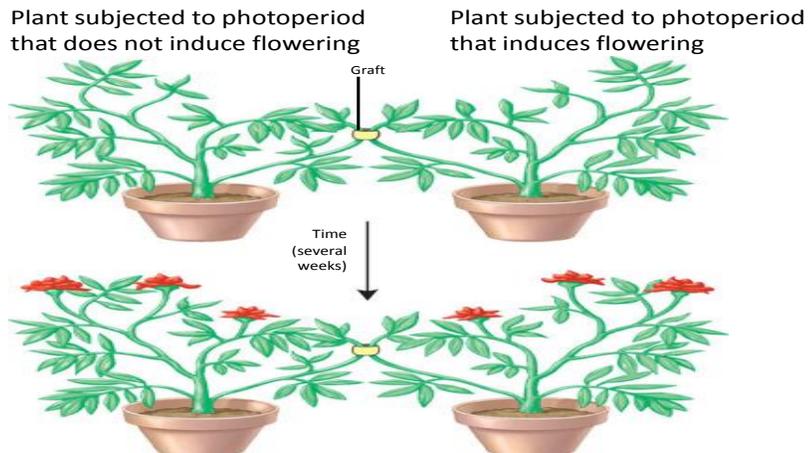
It is now well established that the photoperiodic stimulus is perceived by the leaves. As a result, a floral hormone is produced in the leaves which are then translocated to the apical tip, subsequently causing the initiation of floral primordia.

1. The diffusible substance is probably similar in most plants. If a SDP is grafted to a LDP and they are placed in a short-day photoperiod (that can induce flowering in the SDP), they will both flower, even though the LDP is not in its inductive photoperiod.
2. The nature of floral hormone was named as florigin by Chaikhyan 1968, which can be translocated from leaves to the apical tips situated at other parts of the plant resulting in flowering. There is little direct chemical evidence for its existence. Most evidence is from physiological experiments as described below.

EXPERIMENT

To test whether there is a flowering hormone, researchers conducted an experiment in which a plant that had been induced to flower by photoperiod was grafted to a plant that had not been induced.

RESULTS



CONCLUSION

Both plants flowered, indicating the transmission of a flower-inducing substance. In some cases, the transmission worked even if one was a short-day plant and the other was a long-day plant.

Grafting experiments in cocklebur plants have even proved that the floral hormone can be translocated from one plant to another. For example, if one branched cocklebur plant which has been exposed to short day conditions is grafted to another cocklebur plant kept under long day condition, flowering occurs on both the plants. Obviously the floral hormone has been transmitted to the receptor plant through graft union.

Nature of the Floral Hormone:

Chailakhyan (1936) named this flower inducing chemical substance as Florigen, which can be translocated from leaves to the apical tips situated at other parts of the plant resulting in flowering. Grafting experiments in cocklebur plants have even proved that the floral hormone can be translocated from one plant to another.

For example, if one branched cocklebur plant which has been exposed to short day conditions is grafted to another cocklebur plant kept under long day condition, flowering occurs on both the plants. Obviously the floral hormone has been transmitted to the receptor plant through graft union. But if a cocklebur plant is grafted to another similar plant both of which have been kept under long day conditions, flowering will not occur on either of the two plants.

It has also been indicated that the floral hormone may be identical in short-day and long-day plants. For example, grafting experiments between certain long-day plants and short – day plants have shown that flowering occurs on both the plants even if one of them has been kept under non-inductive photoperiods.

Gibberellins and the flowering response:

It is now well known that the gibberellins can induce flowering in long-day plants even under non-inductive short days. It is also definite that the gibberellins alone do not constitute the 'florigen', but it is usually held that the gibberellins are in some way connected with the overall process of flowering.

Temperature and flowering (Vernalization)**A. Overview.**

Many plants require a cold treatment to induce flowering. This is termed vernalization. Vernalization is common in biennials and winter annuals (such as winter wheat). The effect can be qualitative or quantitative. Vernalization usually works in concert with photoperiod - in other words, vernalization is required to make the plants sensitive to photoperiod. Thus, this acts as a "fail-safe" system to insure flowering at the appropriate time of year (after winter!). The term was coined by Lysenko (1928).

B. Signal.

Cold, actual temperature varies from 1 to 6⁰C.

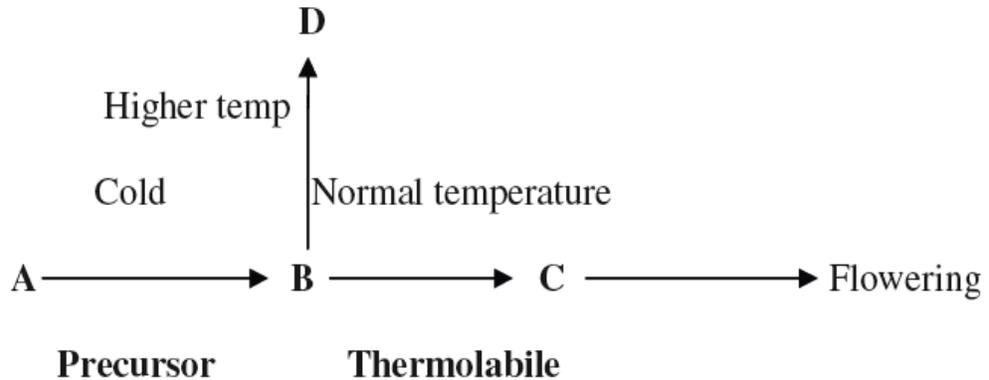
C. Receptor.

1. Some seeds can be vernalized. However, they must be hydrated (dry, unimbibed seeds are insensitive).
2. The cold stimulus is perceived by the apical meristems and all dividing cells including those in roots or leaves may be the potential sites of vernalization.

D. Mechanism

1. Plants can "remember" the signal. In other words, cold-treated plants will grow vegetatively for quite awhile before flowering. This suggests that the induced state must be permanent, or at the least be relatively stable, in many species.

2. A chemical signal may be involved - the transmission of a signal through grafts has been noted with some. This hormone has been termed **vernalin**, but not yet isolated.



According to the hypothesis, precursor A is converted into a thermolabile compound B during cold treatment. Under normal conditions, B changes into C which ultimately causes flowering. But at higher temperature B is converted into D and flowering does not take place (devernalization).

Devernalization:

The positive effect of the low temperature treatment on the vernalization of the plants can be counteracted by subsequent high temperature treatment. This is called as devernalization. The degree of devernalization decreases if the duration of the cold treatment has been longer. However, the devernalized plant can again be vernalized by subsequent low temperature treatment.

Conditions necessary for vernalization:

1. Age of the plant

It determines the responsiveness of the plant to cold stimulus and it differs in different species. In case of biennial variety of henbane (*Hyoscyamus niger*), the plants will respond only when they are in rosette stage and have completed at least 10 days of growth.

2. Appropriate low temperature and duration of the exposure

Most suitable temperature is 1-6°C. The effectiveness decreases from 0 to -4°C. Temperature of -4°C is completely ineffective. Similarly from 7°C the response decreases. Temperature 12°C-14°C are almost ineffective in vernalizing the plants.

3. Oxygen

Vernalization is an aerobic process and requires metabolic energy. In the absence of O₂, it becomes completely ineffective.

4. Water

Sufficient amount of water is also essential. Vernalization in dry seeds is not possible.

IMPORTANCE OF VERNALIZATION:

1. Vernalization increases cold resistance in plants.
2. It reduces the vegetative period of development of plants and induces early flowering.
3. Winter varieties of crop plants can be converted into spring varieties by vernalisation.

Biological Clock:

The various physiological processes do not occur at a constant rate during the different times of the day and night. The rates fluctuates showing peaks and dips at regular intervals. In other words the occurrence of the process is rhythmic. At first glance it may appear that such rhythms may be because of different external factors like temperature, light and humidity which fluctuate during the different times of the 24 hrs day. However, the plants continue to exhibit such rhythms even when held at constant conditions. It means that the occurrence of such rhythms is not because of variations in the external conditions (not exogenous) but appears to be controlled by the plant itself (endogenous). They are called as **endogenous rhythms**.

Most of the endogenous rhythms that occur in plants have a periodicity of frequency of about 24 hrs. That is, this process is repeated once in about 24 hrs and called **circadian rhythms**. Some properties of these diurnal rhythms are demonstrated by the sleep movement of the leaves of legumes. During the day the leaves are horizontal, while during the night the leaves assume a more vertical position.

The other examples of circadian movement in higher plants are cell mitosis, respiration, , enzymes activity and flower petal movement.



PHYSIOLOGICAL BASIS OF TRAINING AND PRUNING:

Pruning is a tool to regulate size and shape of plants to achieve desired architecture of canopy and also reduce foliage density by removal of unproductive branches. Commonly, trees are pruned annually in two ways. A few shoots or branches that are considered undesirable are removed entirely without leaving any stub. This operation is known as 'thinning out'. The other method which involves removal of terminal portion of the shoots, branches or limb, leaving its basal portion intact, is called 'heading back'. Thinning out involving large limbs as in old and diseased trees is called 'bulk pruning'. These operations are carried out to divert a part of the plant energy from one part to another. As trees grow older, they should receive relatively more of thinning out and less of heading back. Heading back tends to make trees more compact than thinning out. If a few of the several branches growing close together on the same parent limb are entirely removed or thinned out, the rest of the branches would grow more vigorously. Thinning out results in lesser new shoot growth but more new spurs and fruit bud formation than corresponding severe heading back.

Pruning is done with the following specific objectives.

- i) To remove surplus branches
- ii) To open the trees – maximum sun light interception, so that the fruits will colour more satisfactorily
- iii) To train it to some desired form
- iv) To remove the dead and diseased limbs,
- v) To remove the water sprouts and
- vi) To improve fruiting wood and to regulate production of floral buds.
- vii) Source sink relation

Season of pruning:

Little differences are likely to result from pruning at different times during the dormant seasons in deciduous fruit trees though in certain cases, earlier pruning causes earlier foliation in the spring. Late pruning during dormant periods is generally not advocated as it leads to more bleeding than earlier pruning. The exposed cut surface in certain cases may provide an excellent opportunity for infection by some pathogens. For this reason, winter pruning is usually preferred to spring pruning as bleeding will be excess in later period. Summer pruning may have a dwarfing effect or an invigorating influence. A light summer pruning may aid in colouration of fruit in certain species. The amount of pruning or severity of pruning which is desirable for mature trees differs in different species. The minimum amount, which is common to all, is the removal of broken or diseased branches and those which cross against each other. Diseased branches should be completely removed from the base of the trunk. In other cases annual pruning may be very light in the beginning but after some years it may become necessary to prune heavily. Otherwise, the trees may lack vegetative vigour and make very little growth. Under South Indian conditions, old non-bearing mango trees are pruned to expose the centre portion to sunlight and also crowded terminal shoots are thinned to one or two shoots during August-September. The pome fruits such as apple, plum, pears and peaches are pruned every year in December, January; Jasmines are pruned to 45 cm height from the ground level during the last week of November. Proper pruning enhances the beauty of almost any landscape tree and shrub, while improper pruning can ruin or greatly reduce its landscape potential. In most cases, it is better not to prune than to do it incorrectly. In nature, plants go years with little or no pruning, but man can ruin what nature has created. By using improper pruning methods

healthy plants are often weakened or deformed. In nature, every plant eventually is pruned in some manner. It may be a simple matter of low branches being shaded by higher ones resulting in the formation of a collar around the base of the branch restricting the flow of moisture and nutrients. Eventually the leaves wither and die and the branch then drops off in a high wind or storm. Often, tender new branches of small plants are broken off by wild animals in their quest for food. In the long run, a plant growing naturally assumes the shape that allows it to make the best use of light in a given location and climate. All one needs to do to appreciate a plant's ability to adapt itself to a location is to walk into a wilderness and see the beauty of natural growing plants.

Pruning, like any other skill, requires knowing what you are doing to achieve success. The old idea that anyone with a chain saw or a pruning saw can be a landscape pruner is far from the truth. More trees are killed or ruined each year from improper pruning than by pests. Remember that pruning is the removal or reduction of certain plant parts that are not required, that are no longer effective, or that are of no use to the plant. It is done to supply additional energy for the development of flowers, fruits, and limbs that remain on the plant. Pruning, which has several definitions, essentially involves removing plant parts to improve the health, landscape effect, or value of the plant. Once the objectives are determined and a few basic principles understood, pruning primarily is a matter of common sense.

The necessity for pruning can be reduced or eliminated by selecting the proper plant for the location. Plants that might grow too large for the site, are not entirely hardy, or become unsightly with age should be used wisely and kept to a minimum in the landscape plan. Advances in plant breeding and selection in the nursery industry provide a wide assortment of plants requiring little or no pruning. However, even the most suitable landscape plants often require some pruning.

Reasons for Pruning

- To train the plant
- To maintain plant health
- To improve the quality of flowers, fruit, foliage or stems
- To restrict growth

Plan Approach to Pruning

- Pruning should follow a definite plan. Consider the reason or purpose before cutting begins.
- By making the pruning cuts in a certain order, the total number of cuts is reduced greatly. The skilled pruner first removes all dead, broken, diseased or problem limbs by cutting them at the point of origin or back to a strong lateral branch or shoot. Often, removing this material opens the canopy sufficiently so that no further pruning is necessary.
- The next step in pruning is to make any training cuts needed. By cutting back lateral branches, the tree or shrub is trained to develop a desired shape, to fill in an open area caused by storm or wind damage or to keep it in bounds to fit a given area. To properly train a plant, one should understand its natural growth habit. Always avoid destroying the natural shape or growth habit when pruning unless maintaining a close watch over the plant, for after a period of time it attempts to assume the more natural growth habit.

- Make additional corrective pruning to eliminate weak or narrow crotches and remove the less desirable central leader where double leaders occur. After these cuts have been made, stand back and take a look at your work. Are there any other corrective pruning cuts necessary? If the amount of wood removed is considerable, further pruning may need to be delayed a year or so. Remove water sprouts unless needed to fill a hole or to shade a large limb until other branches develop.

PHYSIOLOGY OF TRAINING AND PRUNING

Woody plants are pruned to maintain a desired size and shape and to promote a certain type of growth. Ornamental plants are pruned to improve the aesthetic quality of the plant, but fruit trees are pruned to improve fruit quality by encouraging an appropriate balance between vegetative (wood) and reproductive (fruiting) growth. Annual pruning of fruit trees always reduces yield, but enhances fruit quality. Pruning increases fruit size because excess flower buds are removed and pruning encourages the growth of new shoots with high-quality flower buds. Pruning improves light penetration into the canopy, and light is required for flower-bud development, fruit set and growth, and red color development. Pruning also makes the canopy more open and improves pest control by allowing better spray penetration into the tree; air movement throughout the canopy is increased, which improves drying conditions and reduces severity of many diseases.

Pruning fruit trees is somewhat of an art based on an understanding of plant physiology and development. In other words, if we understand how plants grow and how they will respond to different types of plant manipulations, we can alter vegetative growth and fruiting to obtain trees and fruit with desirable characteristics.

A basic understanding of certain aspects of plant physiology is a prerequisite to understanding pruning. Unlike animals, plants continue to increase in size throughout their lives.

There are only two ways plants can grow.

Primary growth is the increase in length of shoots and roots, and is responsible for increases in canopy height and width.

Secondary growth is the increase in thickness of stems and roots.

Both types of growth require cell division followed by cell enlargement and differentiation.

Plant Growth

Meristems are regions of cell division and there are two types of plant meristems. An apical meristem is located at the tip of every shoot and root (Figure 1). As cells divide in these apical meristems, the shoots and roots elongate as cells are piled one on another. Behind the region of cell division is a region of cell differentiation, where cells enlarge and differentiate into various tissues. In the axil of each leaf is a small apical meristem called an axillary meristem that forms an axillary bud, which usually remains dormant until well after the subtending leaf is fully developed. An axillary bud may remain dormant or develop into a lateral branch or a flower.

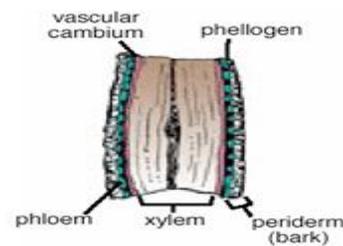
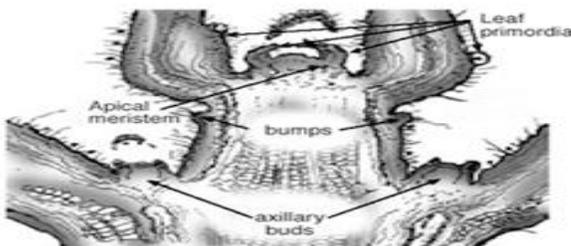


FIG. : Longitudinal section of shoot tip shows an apical meristem, successively older leaf primordia and axillary bud primordia

FIG.: Longitudinal cross-section of a tree trunk shows the vascular and cork cambiums.

There are two distinct layers of meristematic tissue within the stem or root responsible for secondary growth, the vascular cambium and the cork cambium. The vascular cambium is a cylinder of specialized cells, usually five to ten cells thick, running the length of the plant, including the roots, and is responsible for the radial growth of plant parts. Phloem cells are produced to the outside of the cambium and xylem cells are produced to the inside of the cambium. Downward transport of sugars, nutrients, and hormones from the top of the tree to the roots occurs in the phloem tissue. Xylem cells are tube shaped, become hollow and die to form a pipe-like system through which water, hormones and mineral nutrients move from the roots to the top of the tree. Most of the radial growth of woody plants is due to activity of the vascular cambium, but a small amount results from activity in another lateral meristem, the cork cambium, located outside the vascular cambium. The cork cambium (phellogen) together with the cork cells, constitute the periderm: a protective layer of suberized dead cork cells forming the bark. Suberization is the impregnation of cell walls of cork tissue with a fatty substance called suberin. Each season new layers of cells are produced and appear as growth rings when viewed in cross-section. Over time, the xylem cells at the center of the trunk or limb are crushed and become nonfunctional as transport pipes, but they do provide structural support to hold the plant upright. While grafting it is important to line up the cambiums of the scion and the rootstock to ensure a successful graft union.

Buds:

Buds are important to the vegetative and reproductive growth of trees. Fruit tree training and, to a lesser extent, pruning primarily involves bud manipulation. Buds are actually undeveloped shoots. When a vegetative bud is sliced longitudinally during the winter and viewed under magnification, the apical meristem at the tip, leaf primordia (developing leaves), axillary meristems, developing axillary buds, and procambial tissue (tissue that will develop into the cambium) are all visible.

Buds on fruit trees usually have about seven leaves and initial shoot elongation in the spring results from cell expansion. During late June and July some of the shoot apices will flatten out and develop into flower buds. Flower buds are actually modified shoots and the various flower tissues (petals, stigmas, anthers, etc.) are actually modified leaves. Although the process of switching from vegetative to reproductive buds is not fully understood, hormones that can be influenced by environmental factors, stresses, and plant nutrition control the process.

There are several things we can do to influence whether or not a bud becomes a flower bud or remains vegetative. In general, factors that favor rapid growth, such as high nitrogen levels in the shoot tissues, inhibit the development of flower buds. Applying growth-promoting plant growth regulators such as gibberellins usually inhibits flower bud induction, whereas ethylene may promote flower-bud development. Mild stresses such as shoot bending and water stress may also promote flower-bud development.

Producing annual crops of high-quality fruit requires a balance between reproductive and vegetative growth. Fruit producers use various techniques, including pruning, branch bending, and plant growth-regulator sprays, to manipulate tree growth and flowering. Often these techniques affect bud dormancy, so knowledge of buds and bud dormancy is essential if we are to understand how pruning influences tree growth. It is also important to be able to identify the different types of buds on a tree, especially to distinguish between flower and vegetative buds.

Buds may be classified based on location, contents, or activity:

Classification by content several types of buds commonly develop on fruit trees. Vegetative buds only develop into leafy vegetative shoots. Flower buds produce only flowers. Stone fruit trees (peach, nectarine, apricot, plum, and cherry) produce vegetative buds and flower buds. Apple and pear trees produce vegetative and mixed buds. Both leafy shoots and flowers emerge from mixed buds.

a. Classification by location

Terminal buds are located at the tip of a shoot. On stone fruit trees terminal buds are vegetative buds. Terminal buds on apple and pear trees are usually vegetative; however, some varieties such as Rome Beauty produce mixed buds terminally and are referred to as tip bearers or terminal bearers. Most mixed buds on apple and pear trees are formed terminally on short, less than six inch, shoots that terminate with a rosette of leaves. These short shoots are called spurs. Lateral buds form in the axils of leaves and are often referred to as lateral buds or axillary buds. On stone-fruit trees, lateral buds may be either vegetative or flower. Nodes on one-year-old shoots may have one to three buds, some of which may be flower buds and others vegetative buds. Flower buds are larger with tips that are relatively round, whereas vegetative buds are small, narrow, and pointed. In the case of apple and pear trees, lateral buds on the previous season's growth are usually vegetative. However, lateral buds on some varieties, especially on the dwarfing rootstocks, may be mixed buds.

b. Classification by arrangement on the stem

The bud arrangement influences the arrangement of a fruit tree's branches and thus the tree's shape and how easy it is to manage. A node is the joint on a stem where a leaf is or was attached. Axillary buds are located in the axis above where a leaf is attached to the stem. In apples there is usually only one leaf per node, whereas three leaves often arise from a node on peach shoots. When a leaf falls in the autumn, a leaf scar remains just below the axillary bud. Buds are opposite when there are two at the same node but on opposite sides of the stem. Forsythia is an example of a plant with opposite buds. Buds are alternate when there is only one from each node and no one bud is on the same side of the stem as the one next above or below it. Deciduous fruit trees have buds that spiral along a shoot. The spiraling three-dimensional arrangement of leaves around a stem is known as Phyllotaxy and is expressed as a fraction, where the numerator is the number of turns to get to a leaf directly above another and the denominator is the number of buds passed.

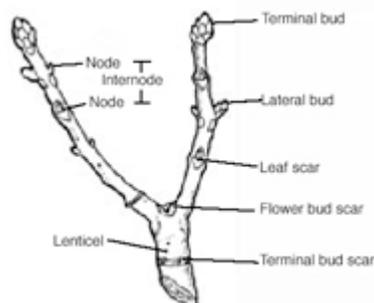


Fig. Section of a limb shows nodes, leaf scars, and different types of buds.

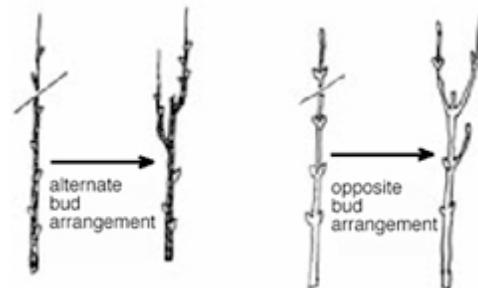


Fig. Shoots with alternate arrangement (left) and opposite arrangement (right).

In each case the shoot has been headed and the diagram to the right of the arrow indicates how the buds respond to the heading cut.

c. Classification by activity

Buds are dormant when they are not visibly growing. When shoots develop around large pruning cuts, they usually are sprouting from dormant buds. Adventitious buds form irregularly on older portions of a plant and not at the stem tips or in the leaf axils. They form on parts of the root or stem that have no connection to the apical meristems. They may originate from either deep or peripheral tissues. For example, shoots often arise from adventitious buds growing from callus tissue around wounds. Root suckers (vigorous upright shoots developing from the roots) develop from adventitious buds on the roots.

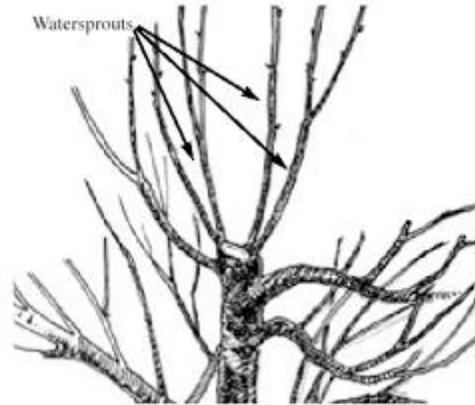


Fig. Watersprouts developing from adventitious buds around a pruning cut used to lower a tree.

Plant Hormones

Hormones are substances produced in very small amounts in one part of the plant and transported to another part where they cause a response. Plants produce a number of hormones that control various aspects of growth, such as stem elongation; dormancy of buds and seeds; flowering; fruit set, growth, and ripening; and the response to light and gravity. While pruning, it is useful to consider the activity of the general types of hormones, promoters (gibberellins and cytokinins) and inhibitors (auxins and abscisic acid). Promoters generally cause bud growth, cell division and elongation, and stem growth. Inhibitors are usually associated with dormancy and inhibit shoot development from seeds and buds and may be involved in flower-bud induction. It is often the ratio of promoters and inhibitors, rather than their absolute concentrations, that determines how a plant will grow. The production of plant hormones is usually controlled by environmental conditions such as temperature or day length. Vegetative growth is usually associated with low ratios of inhibitors to promoters and dormancy is usually associated with high ratios of inhibitors to promoters.

Dormancy is a condition characterized by temporary growth cessation and suppressed metabolism. During the winter trees appear not to be growing, but the tissues are alive, there is metabolic activity, and cells are slowly expanding and differentiating. By early October all the flower parts (petals, stigmas, anthers, etc.) can be seen in a flower bud and vegetative buds contain leaves. During the winter these various tissues continue to enlarge and differentiate. Given favorable growth conditions, some buds will develop into shoots or flowers, but others may remain dormant. By understanding the factors influencing bud

dormancy we often can influence certain aspects of tree growth. Buds of deciduous trees go through several stages of dormancy. Results from dormancy research are confusing because plant physiologists have used different terminology to describe the stages of dormancy. Plant physiologists currently describe dormancy in four stages.

Para-dormancy occurs in the mid to late summer when buds do not grow because inhibitors produced in the leaves and terminal buds inhibit bud growth. Para-dormancy can often be overcome by removing leaves (leaf stripping) along a section of a shoot so the axillary buds develop into shoots. Nurserymen often use this technique to produce trees with lateral branches (feathered trees). Using heading cuts to remove the terminal portion of a shoot will allow several axillary buds just below the cut to develop into shoots. Sometimes an application of growth promoters (gibberellins and/or cytokinins) will induce bud growth.

Sometimes axillary buds do not become dormant and develop into shoots within a few days of being formed. Such shoots are referred to as sylleptic shoots and are fairly common on vigorously growing peach trees, but are rarely produced on apple trees.

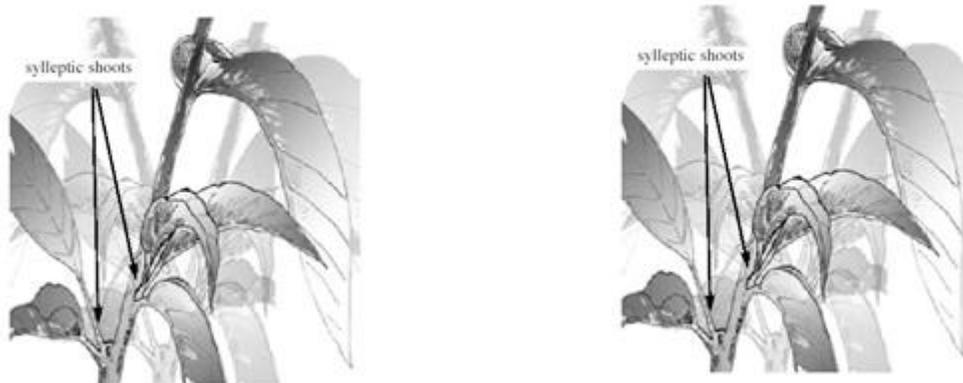


FIG. Sylleptic-shoot growth on peaches during the growing season (left) and during the winter (right). Arrows indicate sylleptic shoots.

Ecodormancy occurs in the early fall, before defoliation, when plants do not grow because the environmental conditions are not conducive for growth. Growth will resume if the plants are exposed to suitable temperatures and day lengths.

Endodormancy occurs during the winter because there are high levels of inhibitors (abscisic acid) within the buds. During this phase of dormancy the trees will not grow even under ideal growing conditions. The concentration of inhibitors declines as buds are exposed to chilling temperatures. Temperatures near 45°F are ideal for chilling, but temperatures between 35° and 55° F will provide some chilling. When the chilling requirement is satisfied, the level of inhibitors within the bud is low enough that growth may commence when environmental conditions are appropriate for growth.

Eco-dormancy occurs in the late winter, usually by mid January, after the chilling requirement has been satisfied. At this time the trees do not grow because conditions are unsuitable for growth. Growth will commence when trees are exposed to warm temperatures.

Apical dominance is a type of para-dormancy, where axillary bud growth is inhibited in the apical meristematic zone. Axillary buds on fruit trees typically remain dormant for a prolonged period while the main shoot continues to grow. Apical dominance has been studied for more than 80 years, and the exact mechanism is not yet fully understood, but it seems to be controlled by the relative concentrations of inhibitors and promoters. Growth of

axillary buds is inhibited by high concentrations of auxin produced by the terminal bud. Auxin moves down the shoot, from cell to cell by gravity, so concentrations are highest near the shoot tip. Promoters are produced in the roots and are transported upward in the tree. Growth of axillary buds may occur at the base of shoots where concentrations of inhibitors are relatively low and concentrations of promoters are relatively high.

The three or four buds immediately below a heading cut usually develop into shoots. Pinching annual plants to induce branching is a form of heading. Another way to overcome apical dominance is to notch buds. Notching involves cutting through the bark to hard wood, with a knife or hacksaw blade at about bloom time, just above a bud. The cut interrupts the downward flow of inhibitors, but not the upward flow of promoters, and releases the bud from dormancy. On vigorous upright one-year-old shoots, notching often successfully overcomes dormancy in about 70 percent of the buds. Sometimes apical dominance can be overcome by spraying shoots with promoters (gibberellins and/or cytokinins) just before bloom time.

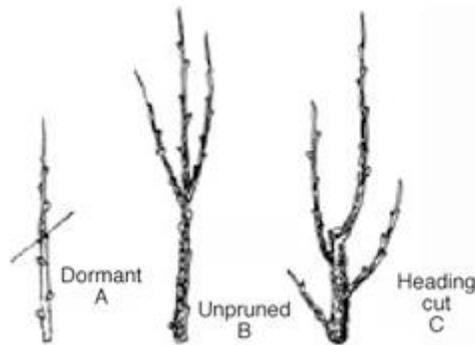


Fig.: One way to overcome apical dominance and inducing branching where we want branching is to head the shoot (A). If the shoot is not headed, the top several buds will develop into shoots (B). If the shoot is headed, several buds below the heading cut will develop into shoots (C).

Shoot bending

Shoots bend in response to an auxin gradient within the shoot. Everyone who has grown plants in the house has noticed that plants tend to grow towards the light. This phenomenon is known as photomorphism and is caused by varying concentrations of auxin in different sides of a stem or shoot. Auxin causes cells to elongate, but auxin is redistributed by light. Therefore, there is a higher concentration of auxin on the dark side of a shoot and the cells on the dark side elongate more than cells on the sunny side of the shoot, causing the shoot to bend towards the light.

The auxin concentration is highest on the dark side of the stem and causes cells on that side to elongate, resulting in stem curvature. Tree fruit producers have noticed a similar phenomenon where the tips of growing branches tend to bend upward, even when the branch was physically oriented to the horizontal. This condition, known as gravimorphism, is also caused by an auxin gradient within the branch in response to gravity. Auxin flows by gravity to the lower side of a limb. The subsequent accumulation of auxin is responsible for increased cell elongation on the underside of the limb, and the growing tip bends upward.

Another consequence of gravimorphism is the development of watersprouts from the upper surface of horizontally oriented limbs. Watersprouts are vertically growing shoots that

develop from the upper surfaces of branches or near pruning cuts. High auxin concentrations on the underside of the limb inhibits growth of buds on the underside of the limb, but the concentration of auxin on the upper side of the limb is inadequate to inhibit bud growth and many of these buds develop into watersprouts. Watersprouts are usually undesirable and their development can be suppressed by orienting limbs no more than 45 degrees from the vertical. Fruit trees are sometimes trained as espalier (tree fence). There are several ways to espalier trees, but one method involves orienting limbs to a horizontal position. This system induces many watersprouts along the length of the branches. Watersprout development can be greatly suppressed by orienting limbs 45 to 60 degrees above horizontal.

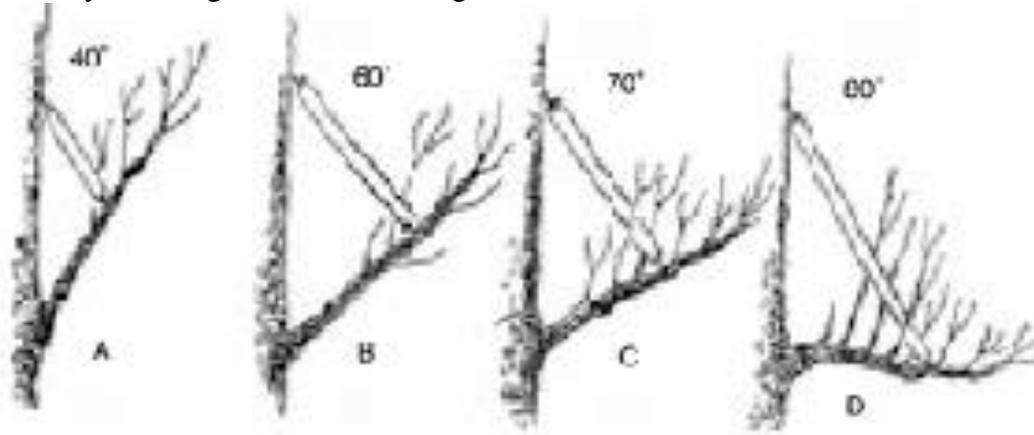


FIG. Auxin distribution within a stem is controlled by gravity. When limbs are oriented from vertical to about 60 degrees from vertical, auxin is distributed fairly evenly around the limb and buds develop into shoots fairly symmetrically around the limb (A and B). Auxin accumulates on the underside of flat limbs (C and D) and inhibits growth of buds on the underside. Auxin concentration is low on the upper side and buds are not inhibited and develop into strong watersprouts.

Reducing tree height by cutting into large diameter branches or trunks often results in the development of vigorous watersprouts around the cut. There are buds buried in the bark that normally remain dormant. However, a severe pruning cut will release these buds from dormancy.

Additional Pruning Facts

Pruning is a dwarfing process pruning increases vegetative growth near the pruning cut and this gives the illusion that pruning stimulates growth. However, the weight of a tree that was pruned annually is always less than the weight of a nonpruned tree.

Pruning reduces yield

Pruning removes wood with flower buds, and thus potential fruit. Yield from pruned trees is nearly always less than yield from nonpruned trees, but fruit quality is improved by pruning. Pruning improves fruit size by increasing the amount of leaf area per fruit. Pruning improves light distribution throughout the tree, which is important for the development of fruit red color and sugar levels.

Pruning delays fruiting

Pruning encourages vegetative growth rather than reproductive growth in young trees. A non pruned tree will always flower and produce fruit earlier in the life of the tree than a pruned tree. The reason young trees are pruned is to induce branches to develop where they are wanted and to develop a strong tree structure that will support large crops as the tree matures, as a tree matures the physiology changes from vegetative growth to reproductive growth. To obtain high annual yields of mature trees, it is important to minimize fruiting until trees have nearly filled their space. Pruning is one technique used to delay fruiting of young trees.

Summer pruning

Summer pruning involves the selective removal of leafy shoots during the growing season. Responses to summer pruning vary with time of pruning, severity of pruning, tree vigor, geographical location, and variety. Several researchers evaluated summer pruning during the 1980s and several general statements can be made about the practice.

Summer pruning reduces within-tree shade and usually improves fruit red color development and sometimes improves flower bud development. Summer pruning removes leaves that produce photosynthates (sugars) for growth of all tree parts. Summer pruning sometimes reduces fruit size and sugar levels. Due to reduced whole-tree photosynthesis, summer pruning suppresses late season trunk enlargement and root growth.

Summer pruning does not suppress shoot elongation the following season. Summer pruning reduces late-season photosynthesis, and theoretically should reduce the accumulation of reserve carbohydrates within the tree that are used for early season growth. However, results from most pruning experiments indicate that the response to a certain type of pruning cut will be the same regardless of the time of year the cut was made.

Canopy Regulation in Fruit Crops:

Canopy management:

Canopy in a fruit tree refers to its physical composition comprising of stem, branches, shoots and leaves. The canopy density is determined by the number and size of the leaves, architecture of stem, branches and shoots. Canopy management of the fruit tree deals with the development and maintenance of their structure in relation to the size and shape for the maximum productivity and quality. The basic concept in canopy management of a perennial tree is to make the best use of the land, the climatic factors for an increased productivity in a three dimensional approach. Tree vigour, light, temperature and humidity play a vital role in the production and quality of the fruits.

The major objective is to achieve maximum productivity in a shortest period without adversely affecting tree health and bearing of the orchard. The natural tree canopy of the fruit tree varies greatly from species to species and cultivar to cultivar. The size, shape and volume of canopy are affected by climate, planting density, rootstock, method of propagation, training, pruning, regularity of bearing, soil type, nutrition, irrigation, intercrop, growth regulators used, diseases, pests, environmental pollution etc.,

The root of the canopy management lies in the fact, as to how best we manipulate the tree vigour and use the available sunlight and temperature to increase the productivity and quantity and minimize the adverse effects of weather parameters. Some of the basic principles in canopy management are as follows.

- 1) Maximum utilization of the light
- 2) Avoidance of the build up of micro-climate congenial for the diseases and pests

- 3) Convenience in varying out the cultural operations, maximizing the productivity and quality
- 4) Economy in obtaining the required canopy architecture.

Light is an important factor in production of fruit. It has a role in flower induction as well as in fruit development through carbohydrate synthesis. While increased assimilates in the shoots is a pre-requisite for flowering in mango and other fruits generally, high yield of quality fruits are attributed to high light interception and distribution in the tree canopy. The fruit yield is related to light interception, whereas fruit quality is a function of light distribution. Light interception is influenced by plant density, canopy shape, canopy leaf area index and can be raised by increasing the density of foliage in the canopy, the height of the tree and number of trees per hectare. Light intensity decreases, within the tree canopy as the outer portion shades the inner canopy. Light exposure influences flower bud differentiation, fruit set, fruit colour and quality. In the canopy management, major emphasis is usually required to reduce the excessive canopy shading and increase the air circulation in the fruiting region.

The practices used to accomplish these objectives are:

- a) Control of tree vigour
- b) Reduction of canopy shading
- c) Training and pruning system to increase light interception and distribution.

Light was found to perform a triggering action in the process of fruit bud differentiation in grapes. Failure of the flowering in mango trees with dense canopies and opening of the canopies through pruning support indirectly the role of light in fruits bud formation in mango. However, the light dependence for the flower bud formation is not the same in different varieties. While, White Riesling variety of the grape requires less light intensity, Thompson Seedless requires less light for the fruit bud formation. Higher light intensities of more than 3,600 ft candles and temperature above 35°C are favourable for the bud fruitfulness in Thompson Seedless grape. The light utilized by the plants for the photosynthesis corresponds to 400 to 700 nm of the electro-magnetic radiation from the sun. Kriedmann and Smart 1971 reported that the photosynthesis in grapes rapidly increases upto the light intensity of 5,000 ft (200 watts/m²). The light compensation point, at which the rate of photosynthesis, is just the equal to the rate of respiration in Thompson Seedless grape is 125 ft candles (5 watts/m²). Leaves at the light regimes of lower than the compensation point are the liabilities to the plant. A leaf absorbs more than 90 per cent of the solar radiation depending upon its thickness. Even if the full sunlight in a given locality is 12,000 ft candles, the third layer of leaves in a tree canopy would receive the light at a lesser intensity than the compensation point. Therefore, the tree canopy architecture has to be so managed that every leaf gets light at the intensities, which are more than the compensation point.

Close planting of the trees and the development of dense canopies may alter the micro-climate around the tree canopy. Temperature and light regimes decrease, while humidity increases. The incidence of powdery mildew will be more under the low temperature and in shaded conditions. *Bortrytis* rot of the bunches was observed to be less in the vines with exposed canopy. Low temperature and the high humidity caused by dense canopies in grape was found to favour the incidence and spread of the downy mildew. The efficacy of plant protection measures will be reduced, when the canopy is dense and the trees are tall. Canopy size and shape should be such, so that the cultural operations could be carried out in an orchard with ease and mechanization of some operations is possible. They

primary aim of the canopy management is to increase the productivity per unit area, quality of the fruit and to reduce the cost of production. The canopy architecture should be easy and less expensive.

Ideal canopy architecture

Ideal canopy architecture should fulfill as many as possible principles involved in canopy management. *i.e.*, the canopy size should be dwarf, spreading and open in mango and guava. In order to obtain more yields per unit area of the land, it is desirable to have the required surface area per canopy volume by increasing the canopy height. But due to inconvenience in carrying out the cultural operations including harvest, the canopy height should be at manageable level.

Tools for the canopy management

Canopy architecture is a natural expression of the genetic makeup of a tree. Genotypes vary in the canopy size and shape. However, the size and shape of the canopy may also be manipulated through various means. Some details of a few of them are given here under.

Training

Training of the perennial trees to the open vase centre is an age old practice to harvest the advantage of the light and ventilation. Basically, the training is a potential tool to manage the canopy architecture of a plant with weak stem like grape vine. Bower system of the training has been found to be the best in tropics throughout the world. Although, it is an expensive training system associated with the reduced light and temperature in vine canopy, increased humidity and disease incidence, it is inevitable for exploiting fully the productive potential of the grape vine in tropics, where the phenomenon of the apical dominance is more pronounced. It is possible to develop as many as 10 shoots/m² by subdividing the apices growing in horizontal plain. Vertical canopies, which envisage the best utilization of the light and the minimization of building up of a high humidity in vine canopy, do not have provision to increase the number of fruiting units per unit area. The best way to manage the canopy in grape vines is to develop diageotropic canopies and increase the fruitfulness of the buds and consequently the cluster:cane ratio.

Pruning

Pruning is a tool to regulate the tree size and shape to achieve a desired architecture of the canopy and also to reduce the foliage density by removing the unproductive branches of a tree. Pruning in mango was favourable for flowering by redistribution of endogenous hormones and increasing the total phenolic contents in shoots. The incidence of mango malformation was also reduced by reducing the foliage density by pruning. In mango annual topping or hedging or the combination of both, effectively controlled tree size but reduced the yields. On contrasts topping plus biannual hedging although controlling vegetative growth to a lesser degree than annual pruning, produced yield similar to those of control trees. Hedging one side per year or all four sides every two years resulted in higher yields than hedging two sides per year.

In Africa for mango size maintenance, pruning is performed shortly after harvest. The aim is to remove the growth which occurred after the previous harvest by heading all of the braches back. Size maintenance pruning is performed by hand or by mechanically hedging and may only be required every second or third year in cultivars or situations where yearly canopy expansion is not substantial.

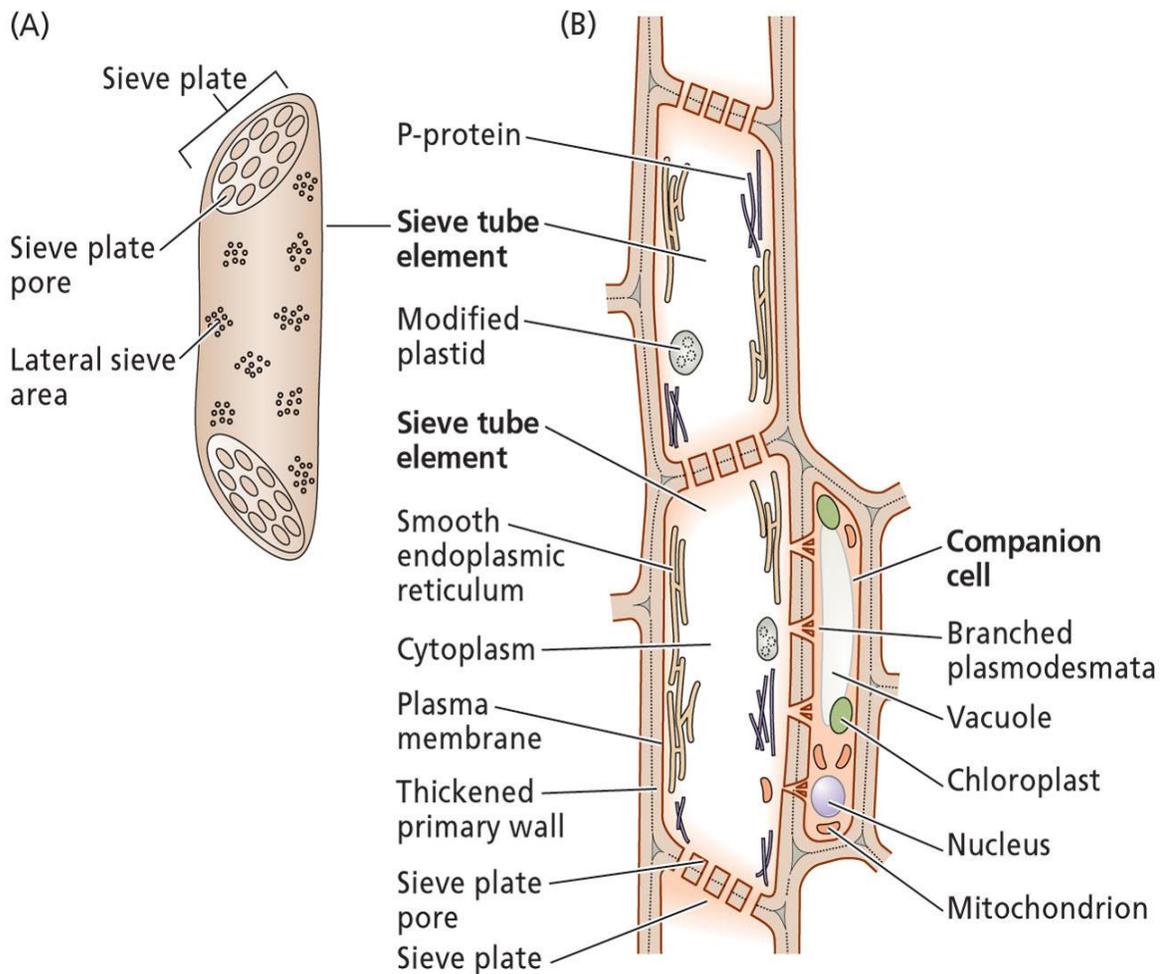
Yield in citrus could also be increased by removing the upright branches and encouraging the horizontal ones by pruning. While, pruning of one-year-old shoots to their half length has been recommended to increase the yields in mandarin, skirt pruning at a length of 1 m could also increase the yield in Washington Navel sweet orange. Pruning and shoot topping are the regular practices to shape the canopy and to promote fruiting and ripening in grape.

TRANSLOCATION OF SOLUTES:

Survival on land poses some serious challenges to terrestrial plants, foremost of which is the need to acquire and retain water. In response to these environmental pressures, plants evolved roots and leaves. Roots anchor the plant and absorb water and nutrients; leaves absorb light and exchange gases. As plants increased in size, the roots and leaves became increasingly separated from each other in space. Thus, systems evolved for long-distance transport that allowed the shoot and the root to efficiently exchange products of absorption and assimilation. Xylem is the tissue that transports water and minerals from the root system to the aerial portions of the plant. The phloem is the tissue that translocates the products of photosynthesis from mature leaves to areas of growth and storage, including the roots.

PATHWAYS OF TRANSLOCATION

The two long-distance transport pathways—the phloem and the xylem—extend throughout the plant body. The phloem is generally found on the outer side of both primary and secondary vascular tissues. In plants with secondary growth the phloem constitutes the inner bark. The cells of the phloem that conduct sugars and other organic materials throughout the plant are called sieve elements. Sieve element is a comprehensive term that includes both the highly differentiated sieve tube elements typical of the angiosperms and the relatively unspecialized sieve cells of gymnosperms. In addition to sieve elements, the phloem tissue contains companion cells and parenchyma cells. In some cases the phloem tissue also includes fibers and sclereids (for protection and strengthening of the tissue) and laticifers (latex-containing cells). However, only the sieve elements are directly involved in translocation. Early experiments on phloem transport date back to the nineteenth century, indicating the importance of long-distance transport in plants. These classical experiments demonstrated that removal of a ring of bark around the trunk of a tree, which removes the phloem, effectively stops sugar transport from the leaves to the roots without altering water transport through the xylem. When radioactive compounds became available, radiolabeled $^{14}\text{CO}_2$ was used to show that sugars made in the photosynthetic process are translocated through the phloem sieve elements. Many structures normally found in living cells, even the undifferentiated cells from which mature sieve elements are formed. For example, sieve elements lose their nuclei and tonoplasts (vacuolar membrane) during development. Microfilaments, microtubules, Golgi bodies, and ribosomes are also absent from the mature cells. In addition to the plasma membrane, organelles that are retained include somewhat modified mitochondria, plastids, and smooth endoplasmic reticulum. The walls are nonlignified, though they are secondarily thickened in some cases. Thus the sieve elements have a cellular structure different from that of tracheary elements of the xylem (which are dead at maturity), lack a plasma membrane, and have lignified secondary walls. As we will see, living cells are critical to the mechanism of translocation in the phloem.



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FIGURE: Schematic drawings of mature sieve elements (sieve tube elements). (A) External view, showing sieve plates and lateral sieve areas. (B) Longitudinal section, showing two sieve tube elements joined together to form a sieve tube.

The pores in the sieve plates between the sieve tube elements are open channels for transport through the sieve tube. The plasma membrane of a sieve tube element is continuous with that of its neighboring sieve tube element. Each sieve tube element is associated with one or more companion cells, which take over some of the essential metabolic functions that are reduced or lost during differentiation of the sieve tube elements. Note that the companion cell has many cytoplasmic organelles, whereas the sieve tube element has relatively few organelles.

Characteristics of the two types of sieve elements in seed plants

Sieve tube elements found in angiosperms

1. Some sieve areas are differentiated into sieve plates; individual sieve tube elements are joined together into a sieve tube.
2. Sieve plate pores are open channels.
3. P-protein is present in all dicots and many monocots.
4. Companion cells are sources of ATP and perhaps other compounds and, in some species, are transfer cells or intermediary cells.

Sieve cells found in gymnosperms

1. There are no sieve plates; all sieve areas are similar.
2. Pores in sieve areas appear blocked with membranes
3. There is no P-protein.
4. Albuminous cells sometimes function as companion cells.

PATTERNS OF TRANSLOCATION: SOURCE TO SINK

Sap in the phloem is not translocated exclusively in either an upward or a downward direction, and translocation in the phloem is not defined with respect to gravity. Rather, sap is translocated from areas of supply, called sources, to areas of metabolism or storage, called sinks. Sources include any exporting organs, typically mature leaves, that are capable of producing photosynthate in excess of their own needs. The term photosynthate refers to products of photosynthesis. Another type of source is a storage organ during the exporting phase of its development. Sinks include any nonphotosynthetic organs of the plant and organs that do not produce enough photosynthetic products to support their own growth or storage needs. Roots, tubers, developing fruits, and immature leaves, which must import carbohydrate for normal development, are all examples of sink tissues. Both girdling and labeling studies support the source-to-sink pattern of translocation in the phloem

SOURCE

A source is any plant part that export carbon. Leaves are the principles sources of assimilates.

SINK

The centers of storage or consumption of assimilates are the “Sinks”. A sink is an organ that has a net import of assimilates which would be used for growth or storage.

All actively growing or metabolizing tissues are sinks.

Source-to-Sink Pathways Follow Anatomic and Developmental Patterns:

Although the overall pattern of transport in the phloem can be stated simply as source-to-sink movement, the specific pathways involved are often more complex. Not all

sources supply all sinks on a plant; rather, certain sources preferentially supply specific sinks. In the case of herbaceous plants the following generalizations can be made.

Proximity: The proximity of the source to the sink is a significant factor. The upper mature leaves on a plant usually provide photosynthates to the growing shoot tip and young, immature leaves; the lower leaves supply predominantly the root system. Intermediate leaves export in both directions, bypassing the intervening mature leaves.

Development: The importance of various sinks may shift during plant development. Whereas the root and shoot apices are usually the major sinks during vegetative growth, fruits generally become the dominant sinks during reproductive development, particularly for adjacent and other nearby leaves.

Vascular connections: Source leaves preferentially supply sinks with which they have direct vascular connections. In the shoot system, for example, a given leaf is generally connected via the vascular system to other leaves directly above or below it on the stem. Such a vertical row of leaves is called an **orthostichy**.

Mechanism of Phloem translocation:

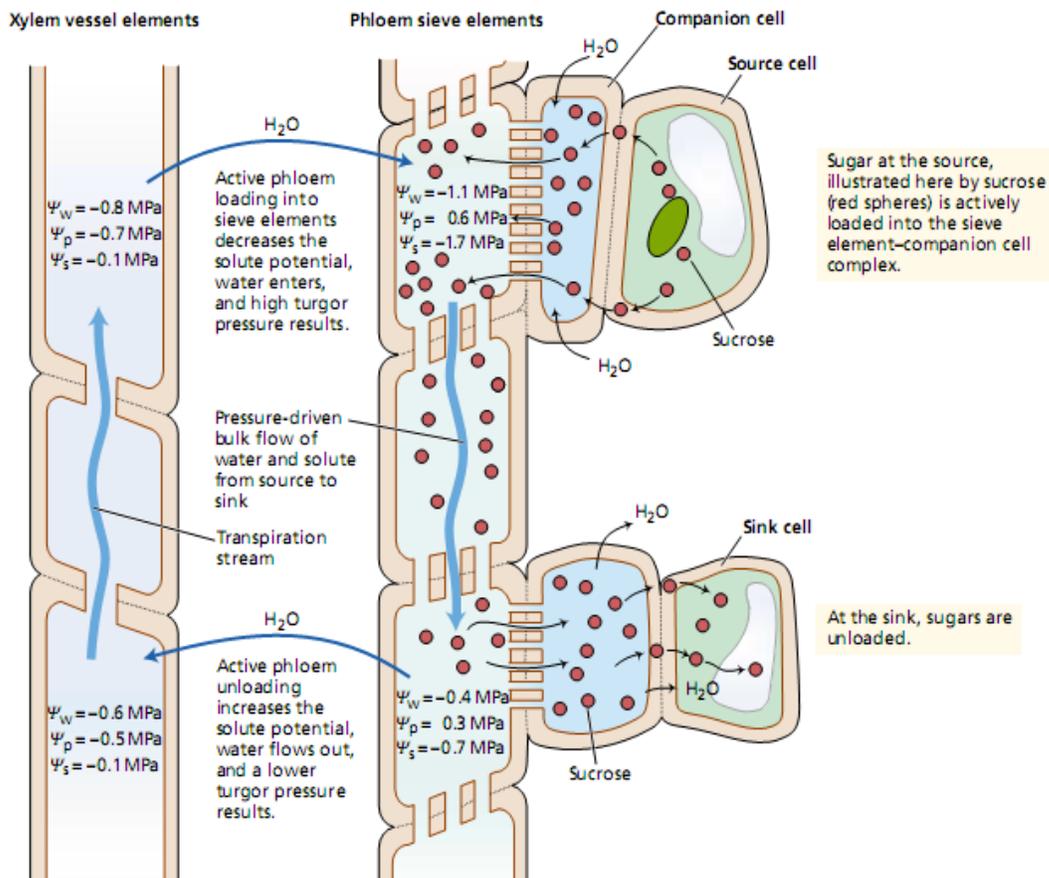
The mechanism of phloem translocation in angiosperms is best explained by the pressure-flow model, which accounts for most of the experimental and structural data currently available. The pressure flow model explains phloem translocation as a flow of solution (bulk flow) driven by an osmotically generated pressure gradient between source and sink. In sources, energy is necessary to move photosynthate from producing cells into the sieve elements. This movement of photosynthate is called **phloem loading**, and transfer of photosynthate from phloem sieve tube element to the cells of a sink is termed as **phloem unloading**. In sinks, energy is essential for some aspects of movement from sieve elements to sink cells, which store or metabolize the sugar. The passive mechanisms of phloem transport further assume that energy is required in the sieve elements of the path between sources and sinks simply to maintain structures such as the cell plasma membrane and to recover sugars lost from the phloem by leakage. The pressure-flow model is an example of a passive mechanism.

The pressure-flow model, first proposed by Ernst Münch in 1930, states that a flow of solution in the sieve elements is driven by an osmotically generated pressure gradient between source and sink. The pressure gradient is established as a consequence of phloem loading at the source and phloem unloading at the sink.

In source tissues, energy-driven phloem loading leads to an accumulation of sugars in the sieve elements, generating a low (negative) solute potential and causing a steep drop in the water potential. In response to the water potential gradient, water enters the sieve elements from nearby xylem vessels and causes the turgor pressure to increase. At the receiving end of the translocation pathway, phloem unloading leads to a lower sugar concentration in the sieve elements, generating a higher (more positive) solute potential in the sieve elements of sink tissues. As the water potential of the phloem rises above that of the

xylem, water tends to leave the phloem in response to the water potential gradient, causing a decrease in turgor pressure in the sieve elements of the sink.

If no cross-walls were present in the translocation pathway—that is, if the entire pathway were a single membrane-enclosed compartment—the different pressures at the source and sink would rapidly equilibrate. The presence of sieve plates greatly increases the resistance along the pathway and results in the generation and maintenance of a substantial pressure gradient in the sieve elements between source and sink. The sieve element contents are physically pushed along the translocation pathway as a bulk flow, much like water flowing through a garden hose.



SOURCE AND SINK CONCEPT

Determination of factors that influence yield is a large and intensively studied area of crop physiology. Yield is the manifestation of all physiological processes occurring in plants.

Since yield is the resultant of dry matter distribution between the different parts of plant, possibilities of changing the distribution of assimilates in crops by physiological manipulation is one of the most promising ways of increasing agricultural productivity. To achieve this, knowledge of source – sink concept is important to understand the direction of transport of assimilates.

The movement of assimilates from source to sink is currently believed to occur as follows:

- 1) The photosynthetic source cell produces the sugars, which can move symplastically or apoplastically to the sieve tubes.
- 2) Phloem loading increases the sugar concentration of sieve tubes above that of the apoplast.
- 3) At the sink, carbohydrates are being absorbed and either actively partitioned into cell constituents (eg. Starch) or changed to other carbohydrates. Phloem unloading lowers the concentration of sugars in sieve tubes.
- 4) The buildup of sugars at the source and the removal of sugar at the sink establish a hydrostatic pressure gradient, which moves water and sugar from sources to sinks.

Thus, higher production of assimilates (source strength), their rapid translocation and utilization in growth and development (sink strength) are some key factors of concern to increase crop yield.

Source strength depends on:

1. Source Size x Source activity
2. Differences in CO₂ fixation (Rubisco & PEP Case)
3. Leaf characters – size, thickness, mesophyll size, compaction, vascular bundle
4. Carrying capacity of sieve element (temp., H₂O, nutrients, hormone)

Sink strength depends on :

1. Sink size x Sink activity
2. Potential capacity of the sink to accumulate assimilates
3. Competition among different sink

Some cases where yield is limited because of source limitation:

- Late anthesis (Long Vegetative phase)
- Indeterminate (Vegetative & Reproductive growth)
- Vegetative growth at Reproductive phase
- Less sink number and size
- Hormonal imbalance
- Any Stress
- Multi-sink demand

Some cases where yield is limited because of sink limitation:

- Low canopy photosynthesis
- Low optimum LAI
- Slow peak LAI (lag vegetative growth)
- Low LAD at filling
- Early leaf senescence
- Stress – nutrients, water

How do you increase source and sink activity:**Source activity is increased by:**

- Recommended dose of fertilizer
- Application of growth regulating substance
- Proper irrigation

- Removal of diseased leaves
- Proper plant protective measures

Sink activity is increased by

- Pruning
- Thinning
- Clipping
- Removal of excess vegetative growth
- Dwarfing in the case of fruit crops (Applying growth retardants)
- Girdling
- Notching
- Application of growth regulating chemicals (booster) at the time flowering, fruit settings, maturation and ripening.
- Application of micro nutrients at the time flowering, fruit settings

HARVEST INDEX

Two useful terms used to describe partitioning of dry matter by the plant are **biological yield & economic yield**. The term biological yield represents the total dry matter accumulation of a plant's system. Economic yield and agricultural yield have been used to refer to the volume or weight of those plant organs that constitute the product of economic or agricultural value. The proportion of biological yield represented by economic yield has been called the harvest index. These terms characterize the movement of dry matter to the harvested part of the plant. (It must be remembered that the biological yield total, often does not include root weight because of the difficulty in obtaining those values)

Crop yield can be increased either by increasing the total dry matter produced in the field or by increasing the proportion of economic yield (the harvest index) or both. There is potential for increasing yields by both methods.

Key points for increasing HI in crop plants:

- Increase biomass production
- Synchronized development of reproductive organ
- Reproductively determinate
- High source strength at the time of sink differentiation
- Reduced growth of non harvestable organ
- Reduced leaf growth at reproductive stage with high LAD
- Optimum LAI and early peak LAI
- More prolonged and faster storage, enhanced competitiveness among of the storage organ
- High photosynthetic rate
- Improved HI by increased size and number of sink organ
- Decline in duration of Vegetative growth and increased duration of reproductive growth

SEED DEVELOPMENT

“A good seed in good soil yields abundant”

-Manu script

Seed: Seed is a fertilized mature ovule containing an embryonic axis (embryo), stored food material (endosperm) and a protective covering (seed coat or testa).

Seed structures:

Living embryo, the most important part of seed, consists of two structures (i) embryonic axis and (ii) cotyledon(s). The embryonic axis is composed of three parts namely (i) radicle (embryonic root), the hypocotyls (point of attachment of cotyledons) and (iii) plumule (the shoot apex with the first true leaves). The three parts of embryonic axis are easy to identify in dicots, but in monocots (especially in the family Gramineae) their identification is difficult. In monocots, there is only one cotyledon, which is reduced and modified to form the **scutellum**. The basal sheath of cotyledon is elongated to take the shape of **coleoptile**, while in some cases (e.g., maize), the hypocotyls is modified to form mesocotyl. The base of hypocotyls sheathing the radicle is termed as **coleorhiza**.

A reserve of stored food, either as cotyledons attached to the embryonic axis or as endosperm tissue, functions as an initial source of nourishment for the embryonic plant until it attains an independent autotrophic existence. The seed coat serves to protect the embryo against adverse environmental conditions and, in some cases, is adapted as a means of seed dispersal. The early developmental stages of the embryo sac are nourished by the cells of the surrounding ovulatory tissue. These cells are originally rich in starch, lipids, and proteins, which are subsequently hydrolyzed to form soluble sugars, amino acids, organic acids, and other metabolically active materials. The ovule is also connected to the main transport system of the plant by a vascular strand through which water, ions, and the other solutes are supplied to the developing seed.

Seed development:

There are many variations in the pattern of seed development when the entire plant kingdom is considered. However, the general process of seed development is almost similar. This includes:

- Embryo development
- Endosperm development
- Seed coat development

1. EMBRYO DEVELOPMENT:

Embryo is a connecting link between two generations of a plant and provides a continuity of genetic material. In most of the Angiosperms, the embryo and endosperm start their development as soon as double fertilization is over. Embryo is diploid in its genetic constitution and is developed from the zygote formed by fertilization between egg cell & one of the sperm nuclei. The embryo or embryonic axis represents the life of a plant in miniature. The size and shape of embryo varies among the plant species. In Monocots where the

endosperm is well developed, the embryo occupies less space of the seed than in dicot species.

2. ENDOSPERM DEVELOPMENT AND COMPOSITION

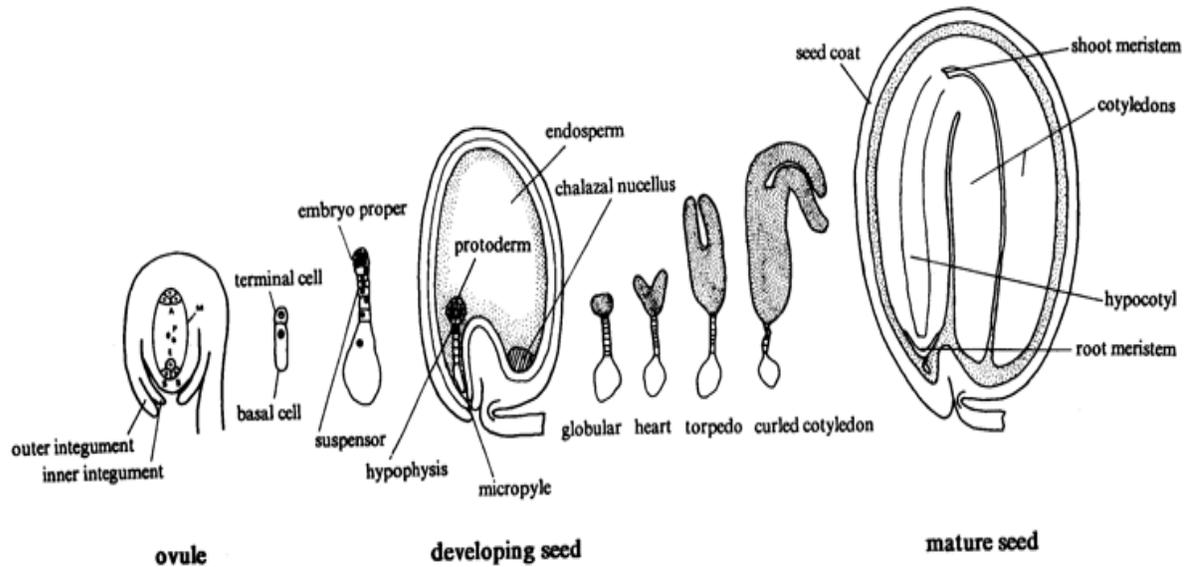
Endosperm tissue is composed of cells with three chromosome sets ($3n$), two from the maternal and one from the paternal parent. This is the situation encountered in many plants, but in the gymnosperms, such as pine and hemlock, the functional equivalent of the angiosperm endosperm has a different chromosome complement and is derived from the female gametophyte, which is composed of haploid ($1n$) cells. Regardless of its origin and chromosome number, the endosperm serves a very special function in nourishing the embryo during early seed formation and maturation and later during seed germination before the embryo develops into an independent plant.

In angiosperms where the endosperm is commonly in the triploid ($3n$) condition, the development of the endosperm generally precedes the development of the zygote. That is, even though the fusion of the egg and sperm nuclei form the zygote ($2n$) and the fusion of the sperm nucleus with the polar nuclei form the endosperm nucleus which may occur simultaneously, the $3n$ endosperm nucleus usually divides to form numerous nuclei before the zygote begins to divide. Frequently the endosperm develops in the free nuclear condition without forming cell wall materials so that a liquid endosperm containing many free nuclei results. Coconut milk is an example of such a liquid endosperm during the early stages of seed development. Probably the endosperm of many other plants passes through a similar free-cell liquid stage. During later stages of endosperm development, cell walls form and a cellular, or solid, endosperm is produced. In many dicotyledonous plants the endosperm is absorbed by the cotyledons of the developing embryo. The food reserves of the cotyledons serves as a nutrient source during germination. In other plants particularly monocots (maize, wheat, etc), the solid endosperm persists and becomes a part of the seed, where it functions to nourish the developing embryo during seed germination.

Seeds with well developed endosperm are called endospermic or albuminous (eg. Rice, Wheat, Castor, opium, Fenugreek) while those with small amounts of endosperm are non- endospermic or exalbuminous (eg. Grams, Peas, Beans).

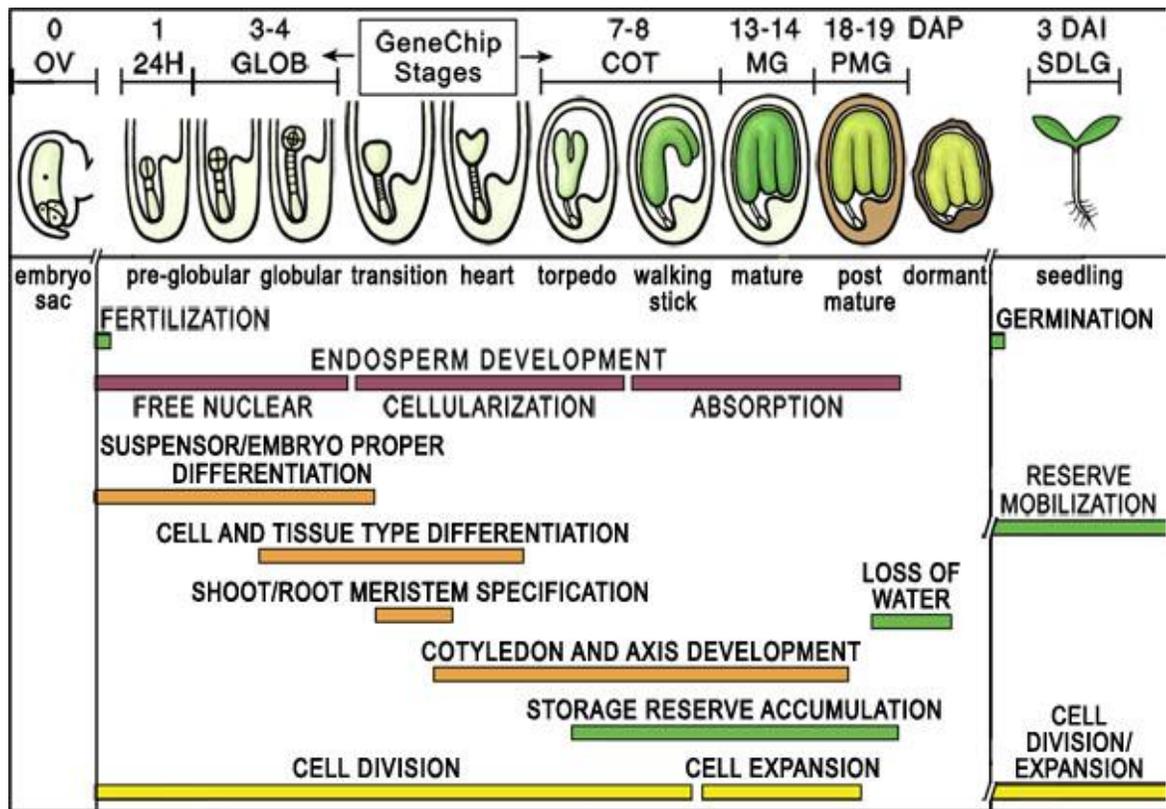
3. SEED COAT DEVELOPMENT:

During seed maturation the outer structure of ovules namely integuments undergo marked recognition to form the seed coat (testa). The seed coat acts as a protective barrier between the embryo and the external environment. The color and the texture of the seed coats vary from species to species and within the species. Almost all seeds bear a scar like point called **hilum**. This is the point at which a seed remains joined with the funicles. The **micropyle**, which is a small hole at one end of hilum, is present in seed coats of many species.



Morphological and biochemical changes accompanying seed development:

The morphological aspects of embryo development (embryogenesis) following pollination, fertilization, and zygote formation have been described for many plant species. Biochemical changes accompanying embryogenesis and seed development are characterized by vigorous anabolic processes, resulting in the formation of new cells, tissues and organs rich in proteins, nucleic acids, carbohydrates and fats. The early stages of seed development, Phase I, involve pollination, fertilization, and zygote formation, processes that contribute very little to dry weight formation but must involve intense metabolic activity. The embryo increase in dry weight as new cells are formed and cellular constituents synthesized. This is a period of intense metabolic activity with a high demand for low molecular weight precursors, such as sucrose, amino acids, fatty acids, nucleosides, organic acids, water, and inorganic ions. The bulk of these materials are supplied by the parent plant through vascular connections, but some also comes from the dissolution of cellular material in the ovule and embryo sac. Phase I comes to an end when the embryonic plant is fully differentiated and cell division ceases. Full-term embryos, excised and nourished by a suitable array of organic molecules and inorganic ions, will continue to develop and form mature plants. The young embryos generally require growth substances in addition to organic and inorganic nutrients. The developing seed is in direct vascular contact with the parent plant. If environmental factors, such as low or high temperature, reduced light, moisture stress, or mineral deficiency, alter the metabolism of the parent plant, the pattern of development during embryogenesis may be altered. Precocious germination is prevented by the action of an inhibitor from ovule tissue. The inhibitor, abscisic acid, may move into the ovule through vascular connections from the parent plant or it may be synthesized in the ovule. Abscisic acid prevents premature or precocious germination. Later in seed development, when vascular connections between the ovules and parent plant are broken by desiccation, low seed water content prevents premature germination.

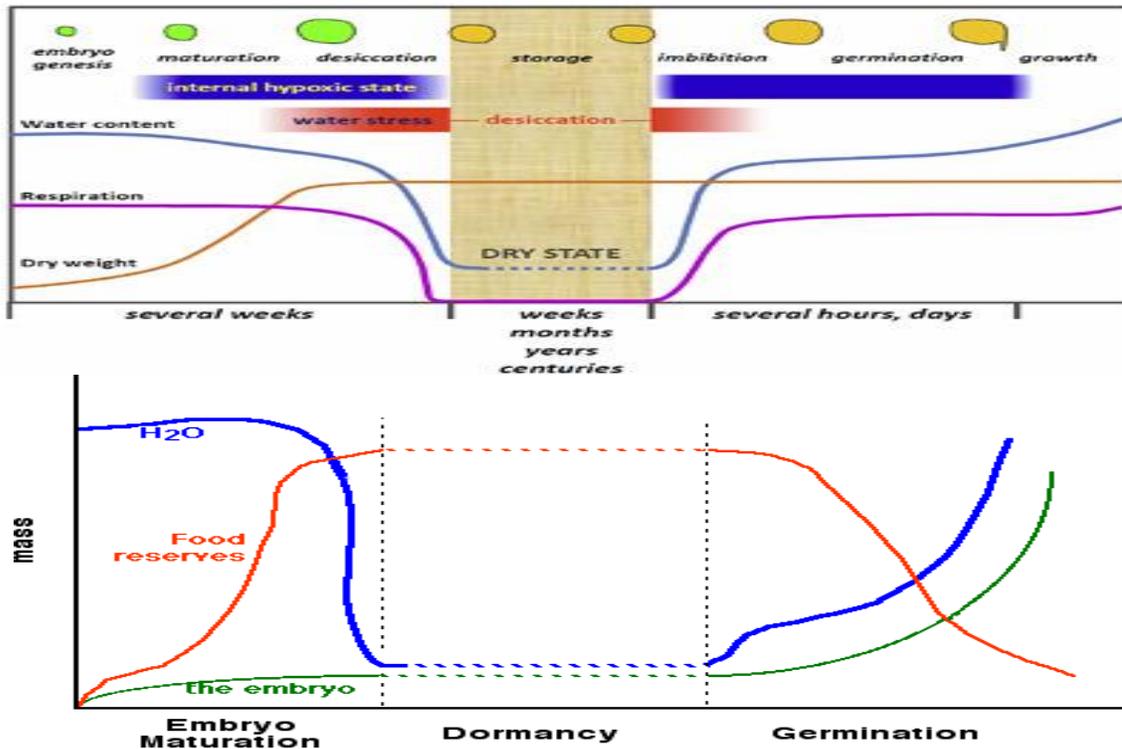


Phase II is the period of maximum seed dry weight increase. The storage materials are synthesized from small precursor molecules from the parent plant. The synthesis and deposition of storage molecules in developing seeds constitute a major sink for carbohydrate and nitrogenous components made by the parent plant. Sucrose, the major product of leaf photosynthesis, supplies carbon skeletons for starch and fats. Moreover, sucrose is a source of carbon skeletons for nitrogenous constituents – amino acids, amides, nucleotides. During seed filling, the demand for carbonaceous and nitrogenous molecules is high and may not be met by current CO_2 , NO_3 , or N_2 assimilation. In such cases, reserve materials in the parent plant may be mobilized and transported to developing seeds. To obtain maximum seed yields, especially in food plants such as maize, peas, soybeans, and beans, it is essential that the leaves and other assimilatory organs of the parent plant be kept active as long as possible. In soybeans, it has been observed that leaf nitrogenous compounds have been hydrolyzed and transported to developing seeds under conditions when the roots cannot supply enough nitrogenous material to support seed filling. The loss of leaf nitrogen leads to premature leaf senescence and the loss of photosynthetic surfaces for carbon assimilation.

Phase II comes to an end as the seed begins to lose water. The synthesis of storage molecules involves the elimination of water molecules, but there appears to be an accelerated process of water loss, possibly through an alternation of membrane structure. Vascular

connections between the developing seed and parent plant are broken so that no water or solutes can move into the seed. Moisture content during seed filling may be in the range of 50 to 60%, but after the desiccation process is under way, water content drops to 10 to 15% at maturity. Water loss is not uniform in all parts of the seed. The embryonic axis, composed of nonvacuolated parenchyma cells, contains relatively little free water, but the structural components are hydrated. Cells in endosperm and cotyledonary tissues, however, contain low amounts of water. Also, the tissues surrounding the seed that develop into seed coats undergo desiccation and sclerification, forming a hard protective structure. With desiccation, the subcellular organelles in cotyledonary cells seem to lose their structural integrity. In addition, organized ribosome's (polysomes) essential for protein synthesis break up into single ribosomes. The entire picture is one of very low metabolic activity, and if seed moisture remains low, further development of the embryonic axis into a mature plant does not occur. The seed is said to be dormant.

CHANGES ASSOCIATED WITH SEED DEVELOPMENT



SEED DORMANCY:

All the viable seeds have capacity to germinate if placed under suitable conditions necessary for germination. But some seeds fail to germinate for sometimes even if placed under the condition favourable for germination. This may be due to some internal factors or due to specific requirement for some environmental factors. During this period, the growth of the seeds remains suspended and they are said to be in rest stage or dormant stage and this phenomenon is called as dormancy of seeds.

Dormancy is defined as physical or physiological condition of the seed that prevents germination in the presence of otherwise favorable conditions for germination.

Dormancy may occur within the embryo (Ground nut) or in the seed coat (Sunflower). The period of dormancy varies from a few days to several months depending on the plant species

Factors causing dormancy of seeds:**1. Seed coats impermeable to water:**

The seeds of certain plants especially those belonging to the families leguminosae, solanaceae, malvaceae, etc. have very hard seed coats which are impermeable to water. The seeds remain dormant until the impermeable layer decay by the action of soil micro-organisms.

2. Seeds coats impermeable to oxygen:

In many plants such as cocklebur and many grasses, the seed dormancy is due to the impermeability of the seed coat to oxygen. However, during the period of dormancy the seed coat gradually becomes more permeable to oxygen so that they may germinate.

3. Immaturity of the Embryo:

In certain orchids, the seed dormancy is due to the immaturity of the embryos which fail to develop fully by the time the seeds are shed. In such cases, the seeds germinate only after a period or rest during which the development of embryo inside the seed is completed.

4. Germination Inhibitors:

In certain seeds, the dormancy of the seeds is due to the presence of certain germination inhibitors like coumarin, ferulic acid, abscisic acid, etc. These may be present in endosperm, embryo, testa or juice or pulp of fruit.

5. Chilling or low temperature requirement:

In certain plants such as apple, rose, peach etc, the seeds remain dormant after harvest in the autumn, because they have a low temperature or chilling requirement for germination. In nature this requirement is fulfilled by the winter temperatures. In such case, the seeds remain dormant throughout the winter season and germinate only in the following spring.

6. Light sensitive seeds

In many species, the germination of the seeds is affected by light resulting in seed dormancy. Such light sensitive seeds are called photoblastic. Seeds of lettuce, tomato and tobacco – are positively photoblastic and germinate only after they have been exposed to

light. On the other hand, the seeds of certain plants are negatively photoblastic and their germination is inhibited by light.

After-ripening: The period of rest after harvest that is necessary for germination is sometimes referred to as **after – ripening period** and the changes that take place during the rest are described as **after – ripening**.

Quiescence: is the phenomenon in which the seeds fail to germinate for want of a particular environmental factor.

Types of Dormancy:

1. Exogenous dormancy

Exogenous dormancy is caused by conditions outside the embryo and is often broken down into three subgroups:

a. Physical dormancy:

This occurs when seeds are impermeable to water or the exchange of gases. Legumes are typical examples of physically dormant seeds; they have low moisture content and are prevented from imbibing water by the seed coat. Chipping or cracking of the seed coat or any other coverings allows water intake. Impermeability is often caused by an outer cell layer which is composed of macrosclereid cells or the outer layer is composed of a mucilaginous cell layer. The third cause of seed coat impermeability is a hardened endocarp. Seed coats that are impermeable to water and gases form during the last stages of seed development.

b. Mechanical dormancy:

Mechanical dormancy occurs when seed coats or other coverings are too hard to allow the embryo to expand during germination. In the past this mechanism of dormancy was ascribed to a number of species that have been found to have endogenous factors for their dormancy instead. These endogenous factors include physiological dormancy caused by low embryo growth potential.

c. Chemical dormancy

This dormancy is caused by the presence of growth regulators etc that are present in the coverings around the embryo. They may be leached out of the tissues by washing or soaking the seed, or deactivated by other means. Other chemicals that prevent germination are washed out of the seeds by rainwater or snow melt.

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.

a. Physiological dormancy:

Physiological dormancy prevents embryo growth and seed germination until chemical changes occur. These chemicals include inhibitors that often retard embryo growth to the point where it is not strong enough to break through the seed coat or other tissues.

Physiological dormancy is indicated when an increase in germination rate occurs after an

application of gibberellic acid (GA3) or after Dry after-ripening or dry storage. It is also indicated when dormant seed embryos are excised and produce healthy seedlings: or when up to 3 months of cold (0–10°C) or warm (=15°C) stratification increases germination: or when dry after-ripening shortens the cold stratification period required.

Seeds with physiological dormancy most often do not germinate even after the seed coat or other structures that interfere with embryo growth are removed. Conditions that affect physiological dormancy of seeds include:

Drying; some plants including a number of grasses and those from seasonally arid regions need a period of drying before they will germinate, the seeds are released but need to have a lower moisture content before germination can begin. If the seeds remain moist after dispersal, germination can be delayed for many months or even years. Many herbaceous plants from temperate climate zones have physiological dormancy that disappears with drying of the seeds. Other species will germinate after dispersal only under very narrow temperature ranges, but as the seeds dry they are able to germinate over a wider temperature range.

Photodormancy or light sensitivity affects germination of some seeds. These photoblastic seeds need a period of darkness or light to germinate. In species with thin seed coats, light may be able to penetrate into the dormant embryo. The presence of light or the absence of light may trigger the germination process, inhibiting germination in some seeds buried too deeply or in others not buried in the soil.

Thermodormancy is seed sensitivity to heat or cold. Some seeds including cocklebur and amaranth germinate only at high temperatures (30C or 86F) many plants that have seed that germinate in early to mid summer have thermodormancy and germinate only when the soil temperature is warm. Other seeds need cool soils to germinate, while others like celery are inhibited when soil temperatures are too warm. Often thermodormancy requirements disappear as the seed ages or dries.

Seeds are classified as having deep physiological dormancy when applications of GA3 does not increase germination; or when excised embryos produce abnormal seedlings; or when seeds require more than 3 months of cold stratification to germinate.

b. Morphological dormancy:

It is because of embryo is 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.

Immature embryos – some plants release their seeds before the tissues of the embryos have fully differentiated, and the seeds ripen after they take in water while on the ground, germination can be delayed from a few weeks to a few months.

c. Combined dormancy:

Seeds have both morphological and physiological dormancy. **Morpho-physiological** or **morphophysiological dormancy** occurs when seeds with underdeveloped embryos, also

have physiological components to dormancy. These seeds therefore require dormancy-breaking treatments as well as a period of time to develop fully grown embryos.

3. Combinational dormancy:

Combinational dormancy occurs in some seeds, where dormancy is caused by both exogenous (physical) and endogenous (physiological) conditions. Some *Iris* species have both hard impermeable seeds coats and physiological dormancy.

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.

Endodormancy, often called 'true' dormancy, which is the prevention of growth due to factors within a meristem. Failure of a bud to grow in early winter due to insufficient chilling, even if it is exposed to warm conditions, is an example of endodormancy.

Paradormancy, which is the suspension of growth caused by factors outside the meristem but within the plant. It is typically an influence of one organ over another, and includes an apical bud preventing outgrowth of a lower bud, which relates to apical dominance. Dormancy imposed by factors in the seed coat is, strictly speaking, a version of paradormancy, because the embryo germinates readily when excised from the seed.

Ecodormancy, which is the prevention of growth due to environmental conditions such as lack of water or temperature extremes. This is also referred to as quiescence or imposed dormancy.

ADVANTAGES AND DISADVANTAGES OF DORMANCY

The survival of natural populations depends mainly on their ability to exploit the favorable and avoid the unfavorable weather conditions to which they are cyclically exposed in their natural habitats. The state of dormancy equips organisms to escape the detrimental effects of adverse natural environments, thereby enhancing their chances of survival. Plants with a long history of domestication generally show much less seed dormancy than wild or recently domesticated species. Thus crop domestication has promoted rapid seed germinability. This may often result in **premature germination** of seeds within ears/pods (**vivipary**) when the crops are exposed to a wet weather favorable for germination just before harvest. In such cases, a pre-harvest rain leads to deterioration in the quality of crop produce, e.g., in wheat, it reduces seed quality and vigor, milling and baking quality, and even grain yield. Therefore, a certain degree of seed dormancy is often deliberately selected for in order to prevent preharvest sprouting in cereals. A brief period of dormancy provides adequate time to farmers to harvest, thresh and store the seeds, thereby avoiding considerable losses.

Disadvantage: The seeds with dormancy cannot be used immediately after harvest for seed purpose.

Methods of Breaking Seed Dormancy:

Various methods have been used by seed scientist and technologists to break the dormancy of seed. Simple and widely used methods are

A. Scarification

Any treatment *i.e.*, physical or chemical that weakens the seed coat, is known as scarification. Scarification method is applied, when dormancy is imposed by hard seed coat e.g. in legumes.

In this method there are various ways to break hard seed coat such as:

1. Seeds are either rubbed on a sand paper manually. At the time of rubbing care should be taken that not to damage the axis of the seed e.g. Green gram & subabool.
2. When seed coat is too hard *i.e.* of woody nature, the seed coat has to be removed completely by breaking it. E.g. Rubber (*Hevea spp.*) seed, India teak wood seed.
3. Soaking treatment: Soaking hard seed coat in concentrated or diluted solution of sulphuric acid for 1 to 60 minutes, it removes seed coat impermeability. E.g. cotton seeds, India teak wood seeds etc.

B. Temperature Treatments

1. When the dormancy is due to embryo factor *i.e.* the seed is incubated at low temp (0- 5°C) over a substratum for 3 to 10 days placing it at optimum temp required for germination. E.g. mustard. – (*Brassica campestris*)
2. Some seeds require a brief period of incubation (from a few hours to one to five days) at 40 to 50 °C before germinating at required temp. (in this method care should be taken that moisture content of the seed is not more than 15% e.g. paddy (*Oryza sativa*).
3. Hot water treatment is also an effective method of breaking hard- seed ness in legumes. In this method the seeds are soaked in water at 80°C temp for 1 – 5 minutes (depending up on the type of seed) before putting for germination.

C. Light Treatments:

Some seeds do not germinate in dark thus it provides continuous or periodic exposure of light is essential e.g. Lettuce (*Lactuca sativa*) requires red light (660nm) or white light is essential for germination to occur.

D. Treatments with growth regulators & other Chemicals:

Endogenous dormancy may be due to presence of germination inhibitors. Application of low level of growth regulators (*i.e.* Gibberellins, Cytokinins and Ethylene etc) may break the seed dormancy. Most widely used growth regulators are gibberellins and kinetins. Among other chemicals potassium nitrate (0.2%) and thio – urea (0.5 to 3%) are widely used for breaking seed dormancy

SEED GERMINATION

The process of seed germination starts with the imbibition of water by seed coat and emergence of growing root tip of embryo. The optimum conditions for seed germination are availability of moisture, O₂ and optimum temperature.

Physiological and biochemical changes associated with seed germination:

Physiological changes :

1. Water uptake

Seed germination starts with the imbibition of water by dry seed coat. Due to imbibition of water the seed coat becomes more permeable to O₂ and water and less resistant to outward growth of embryo. After imbibition, the inner contents of the seed increase in volume, thereby exerting pressure on the seed coat leading to rupture of the seed coat. The plumule and radical emerge thereafter.

2. Respiration

After initiation of germination process, enormous energy is required for various biochemical changes which are met through rapid increase in respiration rate. Sucrose is probably the respiratory substrate at this stage which is provided by endosperm. In oilseeds and pulses, the lipids and proteins respectively are converted into sucrose by suitable biochemical reactions.

3. Mobilization of reserve materials

As germination progresses, there is mobilization of reserve materials to provide.

- i) Building blocks for the development of embryo
- ii) Energy for the biosynthetic process
- iii) Nucleic acids for protein synthesis and embryonic development

Biochemical Changes:

1. Carbohydrates

Insoluble carbohydrates like starch are the important reserve food of cereals in the endosperm. During germination, starch is hydrolysed first into maltose in the presence of α -amylase and β -amylase and then maltose is converted into glucose by maltase. The glucose is further converted into soluble sucrose and transported to growing embryonic axis. During germination, the embryonic axis secretes gibberellic acid, into the aleurone layer which causes synthesis of α -amylase.

2. Lipids

Many plants like castor bean, peanut, etc, store large amount of lipids or fats as reserve food in their seeds. During germination, the fats are hydrolyzed into fatty acids and glycerol by lipase enzyme. Fatty acids are further converted into acetyl – COA by the process of β -oxidation. The acetyl COA is further converted into sucrose via glyoxylate cycle and is transported to the growing embryonic axis

3. Proteins

Some plants store proteins as reserve food in their seeds. Proteins are hydrolysed into amino acids by peptidase enzyme. The amino acids may either provide energy by oxidation after deamination (removal of amino group) or may be utilized in the synthesis of new proteins.

5. Inorganic nutrients

A number of inorganic nutrients such as phosphate, calcium, magnesium and potassium are also stored in seeds in the form of phytin. These stored nutrients are liberated during germination due to the activity of various phosphatases including phytase..

Emergence of seedling out of the seed coat:

First the radical comes out and grows downward, then plumule comes out and grows upward. Due to continued growth of this seedling, the plumule comes out of the soil, exposed to light and develops its own photosynthetic organs. Until the seedlings starts producing assimilate by its own photosynthetic organs, the reserve food available in the seed is sufficient to sustain the seedling growth.

Splitting of seed coat may take place either 1) by imbibitional pressure 2) by internal pressure created by the growing primary root 3) by hydrolytic enzymes which act on cell wall contents of seed coat and digest it eg. Cellulase, pectinase etc and sometimes, the seed coat may be extensively damaged by the activity of micro-organisms in the soil.

REGULATION OF FRUIT SET AND DEVELOPMENT, FRUIT RIPENING

The generic term 'fruit' covers a wide range of structures, all supporting and protecting seeds, but where the various parts have developed from the original fertilized flower in various distinctive ways. In the simplest form, ovary walls grow along with seeds, and as they develop, the ovary walls dry out to become a pod (legume) or capsule (poppy). In others (particularly fleshy fruits), the main structure can arise by exaggerated development of a particular part of the original floral unit. These include ovary wall or central axis, the receptacle that supports anthers and ovary, or even petals and sepals. In morphological terms, fruits are structures that develop from fertilized or stimulated ovules, plus associated floral parts that originate from the parent plant.

Mechanistically, a fruit is a single dispersal unit which includes seeds and associated tissues, developed as a single body. This broad description includes structures derived from a single ovary (as in simple fruits such as apple, avocado and mango) as well as compound fruits where separate ovaries are joined (an aggregate fruit such as blackberry and cherimoya) or where separate flowers are collected into a single structure (pineapple and breadfruit).

During fruit development, an ovary wall becomes a pericarp: either dry as in a dehiscent pea pod and the indehiscent caryopsis of barley or fleshy as in berries (grapes). Three morphologically distinct strata are present and developed to varied degrees: exocarp (fruit skin), mesocarp (fruit flesh) and endocarp (inner cell layers).

An exocarp will develop a cuticle and may exhibit a variety of morphological features such as coarse hairs (kiwifruit) or fine hairs (peach). Exocarp plus cuticle restrict gas exchange, and determine general appearance of ripening fruit. Most cuticles are highly impermeable to gases, so that water vapour, O₂ and CO₂ diffuse mainly via either stomata or lenticels or by mass flow through cavities at the calyx and stem ends of fruit.

Mesocarp tissues usually represent the fleshy part of a fruit, and commonly hold chloroplasts and starch grains. In fleshy fruits such as berries (e.g. tomato, kiwifruit and grapes) this tissue typically comprises large parenchyma cells and contains the main vascular network.

Endocarps are less common, but typically develop as a dense hard case around a seed, as in peach, apricot or macadamia.

An ovary must be stimulated in some way for fruit growth to occur; this is normally by pollination and fertilization. This important principle was established as early as the 1960s when Nitsch showed that gibberellins and auxins are involved in the pollination stimulus. Subsequent hormone production by the fertilized ovary is critical to stimulating fruit development. By implication, a suitable balance of growth regulators applied to unpollinated fruitlets can result in fruit set, and in practice auxin and gibberellins GA₄ and GA₇ are very effective in setting parthenocarpic (seedless) fruit.

Fertilization is generally crucial for fruit set and pericarp development. As fertilized ovules develop into seeds, this influence on pericarp growth continues where production of hormones by the endosperm and developing embryo promotes pericarp growth. The importance of seeds as sources of hormones for initiation and stimulation of fruit growth is implied by fruit response to exogenous hormones in parthenocarpic systems (development of fruit without seeds).

Limitation of Fruit set:

Fruit set affects the productivity of fruit crops. There are three main causes of limitation of fruit set-

1. It may be due to limited pollination
2. It may be due to limited nutrients
3. It may be due to abscission of flowers and young fruits.
4. Receptivity of the female parts to the pollen. This receptive period may last long for only a few hours (as in mango) or for over a week (as in tomato).

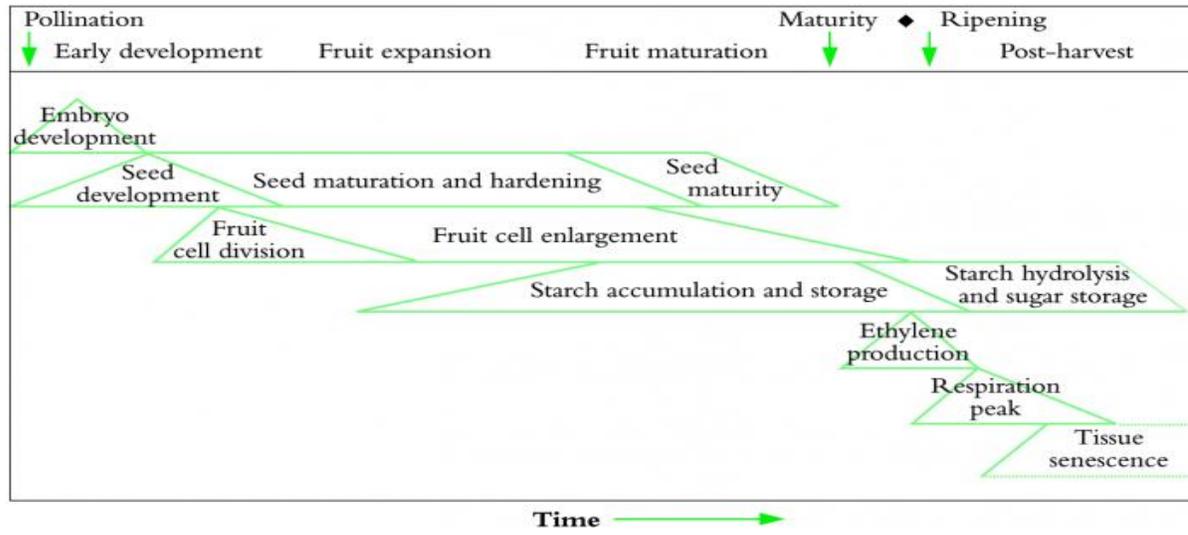
PHYSIOLOGICAL DEVELOPMENT OF FRUITS:

As a general principle, fruit development in terms of weight and volume tends to be sigmoidal. A period of very rapid cell division, but very little increase in fruit size (stage I), is followed by a period of rapid increase in size as small, newly differentiated, dense cells develop vacuoles and assume their roles as specific tissues (stage II). In the final stage, as the fruit reaches physiological maturity, increase in size slows and may even stop, although biochemical changes may continue (stage III). There are about as many variations on this pattern as there are different types of fruit, but the sigmoidal mode is usually discernible.

HORMONAL CHANGES DURING FRUIT DEVELOPMENT:

The gibberellin content in seed increased rapidly during early seed growth and declined as growth decreased. The seed was the major source of gibberellin in the fruit, the pericarp containing only traces. Cytokinins were present both in pericarp and seed. During the single period of rapid growth in fruit and seed, cytokinin concentrations increased rapidly at two periods. The first rapid increase in cytokinin concentrations precedes the period of rapid cell division and cell enlargement and the second increase coincides with the period of rapid cell enlargement only. The level of ABA-like inhibitor was high in the preceding pollination which corresponded with the period of slow growth in fruit and heavy fruit drop. During the rapid period of fruit growth, the level of inhibitors decreased and that of promoters increased. However, in maturation and slow fruit growth period, the levels of both the growth promoters and inhibitors were low. Thus all the growth promoters play their role in the growth of the fruit.

SEQUENTIAL EVENTS OCCURRING IN FRUIT DEVELOPMENT



PARTHENOCARPY

In botany, the formation of fruits without seeds. This phenomenon, of no obvious benefit to the plant, occurs naturally in some plants, such as bananas. It can also be induced in some fruit crops, either by breeding or by applying certain plant hormones.

FRUIT RIPENING:

Ripening may be defined as those nonreversible, diverse, physical, chemical and qualitative changes that render the fruit attractive for consumption at the transition phase following maturation.

After a period of growth, fruit undergoes some characteristic qualitative changes leading to edible state. These changes are collectively referred to as fruit ripening. Some important events in fruit ripening are as follows:

1. Changes with ripening.
2. The respiratory climacteric
3. Hormonal controls of ripening.

Changes with ripening:

The general changes that occur during the process of ripening of fruits are,

- a. Softening of fruit
- b. Hydrolytic conversion of complex storage materials into simpler forms
- c. Changes in pigments and flavours.

Softening may be a detrimental quality in some fruits like cucumber, squashes which are consumed in unripe state. In others, it is an essential component in the development of optimum quality. With the progress of ripening the fruit softens. The softening is due to enzymatic hydrolysis of polysaccharides. The cell wall is made up of cellulose, hemicellulose, calcium pectate, polyuronides, and glycol protein. The important cell wall

hydrolyzing enzymes like pectin methyl esterase (PME), poly galacturonase (PG) and cellulase increases during ripening and the dissolution of middle lamella is observed. This is accompanied by increase in the enzyme PME. Hydrolytic changes in the fruit during ripening usually lead to the formation of sugars. Such changes show different rates in different fruits, e.g. banana ripens extremely fast, apple shows gradual ripening and citrus fruits show very slow changes.

- a) Changes in pectin composition
 - b) Possible alterations in other cell wall components
 - c) Hydrolysis of storage materials
- Texture

During ripening of fruits, some qualitative changes occur such as change in pigmentation, production of flavour and depletion of astringent substances. The changes in pigments in fruits are normally the loss of chlorophyll and the development of carotenoids. There may be changes in colour due to moderate loss of chlorophyll with little or no formation of carotenoids as in banana or due to complete formation of carotenoids, as in oranges. In the ripening fruit, there is a fast disappearance of chlorophyll accompanied by accumulation of red and yellow carotenoid pigments in the chloroplast. As the tomato fruit matures, the predominant carotenoid that is synthesized is **carotene**. Some fruits like grapes, pomegranate produces anthocyanins when mature. In tomato another pigment accumulates during ripening is **Lycopene**. Chlorophyll is lost due to chlorophyllase activities. The newly developed pigments may be carotenes as in papaya or anthocyanins as is strawberry and these are synthesized in the presence of sunlight and with the involvement of phytochrome.

Changes in pigmentation

- a) Degradation of chlorophyll
 - b) Unmasking of existing pigments
 - c) Synthesis of carotenoids
 - d) Synthesis of anthocyanins
- Color

During ripening, starch hydrolysis occurs, and sugar accumulates. For example starch content of banana decreases from the initial 21% to about 1% in ripened fruit. This is accompanied by accumulation of sugars mainly sucrose to the extent of up to 20% by fresh weight. The taste of the fruit depends upon the sugar acid ratio and also on the absolute level of sugar and acid contents. The pH of all the fruits is in the acidic range.

Change in carbohydrate composition.

a) Starch conversion to sugar

b) Sugar inter conversions

Production of aromatic volatiles

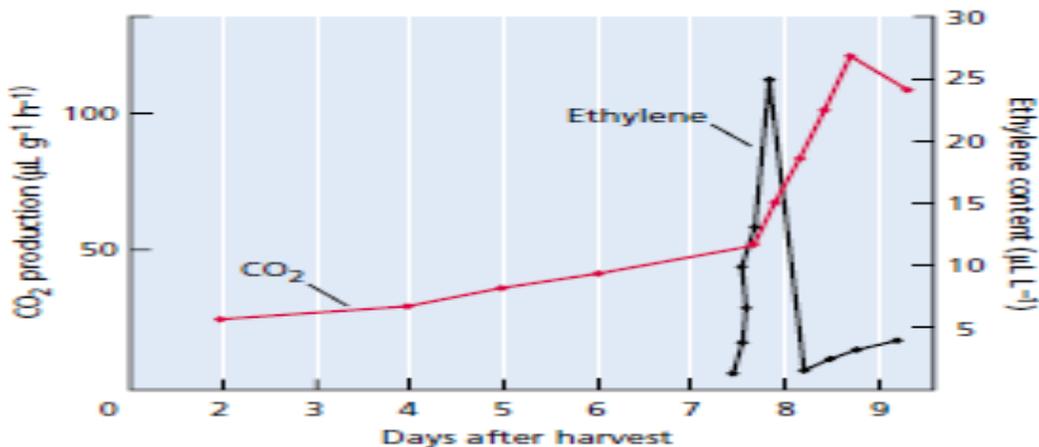
Changes in organic acids

Flavor

The Respiratory Climacteric:

The period of occurrence of respiratory climacteric peak in fruits show variation in different fruits, e.g. at the time of optimum eating quality as in pear, it slightly precedes this optimum in banana and apple or just before the fruit is fully ripe as in tomatoes. Earlier it was suggested that climacteric is associated with the hydrolysis of food reserves, but it has not been found true in all cases, e.g. orange, lemon, grapes and fig in which case climacteric rise in respiration is not found during fruit ripening. The process of fruit ripening proceeds slowly in these crops. Hence, these fruits are termed as non climacteric fruits.

The respiratory peak and ethylene content in typical climacteric fruit



As regards occurrence of climacteric, fruits may be divided into two types:

1. Climacteric fruits
2. Non climacteric fruits

In non-climacteric fruits, the rate of respiration remains steady during their ripening.

Climacteric rise has been found affected by low oxygen and increased concentration of carbon dioxide. Both these factors prevent climacteric rise and thus improve storage quality of fruits. Storage of fruits in polythene bags produces nearly the same effect because plastic can lower oxygen and elevate carbon dioxide around fruits.

Ethylene has been established as a ripening hormone. Massive doses of ethylene can bring about ripening changes in immature fruits. So, it is the hormone which plays the most powerful regulatory role in ripening. It has been observed that a rise of ethylene level occurs at the onset of the climacteric rise and can be assigned the role of the trigger of ripening. They proposed that the onset of ripening is associated not only with a rise in the ability to biosynthesize ethylene but also a marked increase in ethylene responsiveness. It has also been found that ethylene can induce a respiratory climacteric in some leaves and develop many of the pigments commonly developed in fruit ripening. In general, ethylene may be bringing about the formation of new types of enzymes in fruits. However, ethylene is not a universal ripening hormone. Some climacteric fruits like strawberry and citrus have no effect on their ripening by the ethylene treatment.

Application of ethephon promotes degreening and early ripening in grape, tomato, coffee, peach, pear, plum and citrus. Smoking is commercially employed to hasten degreening and ripening of banana and mango. Calcium carbide release acetylene, on hydrolysis of which hasten ripening process.