

Physiological Aspects of Flowering, Fruit Setting, Fruit Development and Fruit Drop, Regulation and Their Manipulation- Review

Abstract:

The physiology of flowering and fruit setting involves the changes in the characters of cells proliferating in the meristematic tissues of the shoot owing to the specific gene action and change in the phyto-hormones level. Flower formation is a transition phase in the life cycle of a plant. The alteration of vegetative apex into reproductive structure results in flowering initiation. The reduction of shoot meristem starts development of sepals, petals, stamens, carpals instead of leaves. The plant must attain specific state of 'ripeness to response' before it flowers. Once the stage is reached, then it can induce to flower. The flowering is closely linked to the diverse environmental conditions in which each species has evolved. The effects of the large number of factors that influence the proportion of bud giving rise to flowers have generally been interpreted in terms of an inbuilt propensity to flowering and interference with attainment of this.

Comment [R1]: The main objectives and result of the review article should be informed

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Introduction:

Physiology of Flowering

The flower bud differentiation is considered to be the most significant revolving point in flowering, and the life cycle of plant shifts from vegetative to reproductive growth. The phenomenon of switching plant growth from vegetative to reproductive phase is called flowering. The activation of flowering genes are responsible for initiation of flowering in plants and is prompted by environmental factors. The flowering only arises when plants reach a specific age. The process of flowering is divided into two major developmental processes which takes place in two consecutive growing seasons. The two major developmental processes include the initiation and development of flower buds during the summer and fall of one season. Moreover, the flowering process itself occurring in early spring of next season. The seedling trees takes years to reach flowering age. The non-flowering period of young seedlings is called *juvencity*. Seedlings of most fruit trees do not produce flowers, before they reach 3-7 years of age (Visser et al. 1976). The ecological factors responsible for the activation of genes causing flowering are photoperiodic conditions, low temperature and various other stresses. Photoperiodic flowering regulated by photoperiod and vernalization regulated by low temperature have been well studied. It can be studied under the following heads:

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1. Factors in the bud foremost to flowering: Three factors were proposed to happen during the transition phase from bud to flowering i.e. induction, evocation and initiation (Metzger, 1987).

The period when flowering stimulus is produced is called floral induction. Searle (1965) explained the induction state as a physiological condition of tissues which is prompted by external impacts such as photoperiod, chilling temperature and water stress conditions, increasingly towards floral expression even under subsequent non-initiating conditions.

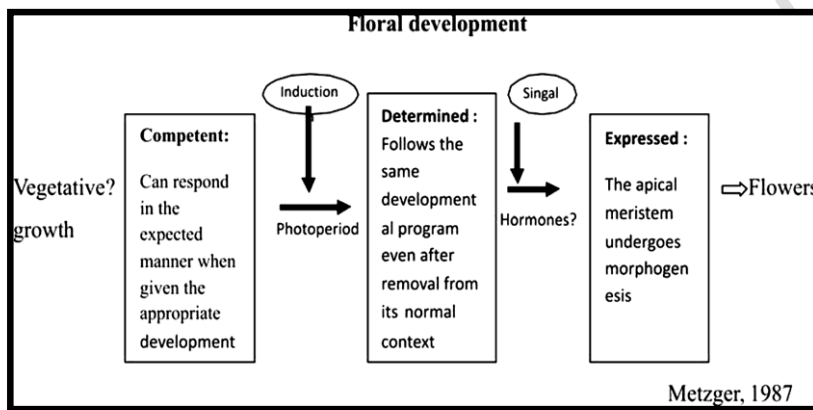
Evocations: The reception of flowering stimulus by shoot apical meristem is permanently devoted to form the primordia for flower bud is called floral evocation (Metzger, 1987). After induction and prior to formation of flowering primordia in the apical meristem of photoperiodic plants, the fluctuation of protein

complements has been analysed.

On the other hand, the floral evocation process contains two development situations: competent and determined. A cell or group of cells is said to be competent if it can revert in the predictable manner when given to a suitable developmental signal.

Initiation: In this process, the evoked buds detectible as a flower bud and thus devoted in reproductive development. The initiation process cause broadening and flattening of the growing point with concomitantly emerging lobes.

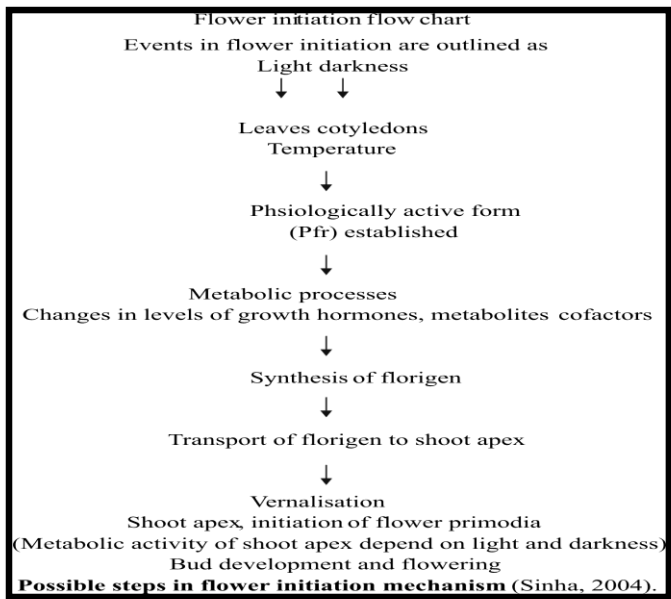
Chart 1 Role of induction and signal in floral development



2. Distinction of the growing points: The conversion of development phases from vegetative to reproductive phases are usually manifested by the intensification of cell division within the central zone of the shoot apical meristems. The intensification of cell division leads to an increase in the size of shoot meristem to develop various flower parts such as sepals, petal, stamens and carpels in place of leaves. The primary noticeable change found in the growing points of the buds is cumulative synthesis of DNA and RNA. (Buban and Faust, 1982). Normally 8-14 days are essentially required from the beginning of histological differentiation to the appearance of lower meristem in temperate fruits. The subsequent development of the flower meristem is relatively rapid. The entire process of flowers and differentiation may take 54-112 days depending on the species.

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Chart 2. Steps in flower initiation mechanism



Fruit Setting

The fruit set plays a significant character in modern fruit production. A large yield of fruit can only be expected if conditions for pollinations for pollination and fruit set are favorable. The fruit set involves different steps; the first step is the transfer of pollen to a receptive stigma. This transfer may be natural or artificial, followed by germination and pollen tube growth. These processes are affected by environmental factors, mineral nutrition, and the genetic makeup of the tree. Concomitantly, the mature embryo sac must develop at the base of the style. Then successful fertilization must occur followed by growth of the embryo. The successful occurring of these steps results in overall process called 'fruit set'. Fruit can set and grow to full size without fertilization, the production of fruit without pollination is termed as parthenocarpy. However, a small degree of parthenocarpy is observed in many fruit species, most widespread in pears among the temperate zone fruits. The degree of parthenocarpic fruit set in some of the pear varieties is significantly inclined by various environmental conditions. In fruit plants, the process of fruit development and seed set is generally taken place in a very coordinated manner resulting from pollination and subsequent double fertilization in the flower ovule. The final fruit shape is totally depended on the number of contributive factors, kind and location of various floral organs, and how the different tissues **perform functions within them. During the formation of the dry *Arabidopsis thaliana* fruit, the ovary containing two fused carpels enlarges to form a silique with localized dehiscence zones at each carpel boundary that split open to release the mature seeds. By contrast, the ovary of tomato fruits enlarges after the process of fertilization and the locule space round the emergent seeds fill with pulp to form the fleshy fruit.**

The pollinated flower develops to a fruit, and the fertilized ovules grow to seeds due to an intense synthesis of growth substances. They appear first in the developing endosperm of the seed primordia (ovules) and penetrate the wall of ovary (the future pericarp) as well as the other parts of the fruit primordium including the peduncle. The centre of organic synthesis of the fruit primordium keeps being the growing embryo and the surrounding endosperm. The intense cell division and growth of the tissues absorbs a lot of organic matter of the reserves competing with the vegetative organs, consequently, an interaction between the different parts of the organs of the tree is building up. Not only the fate of the growing fruit, its size and quality but also the physiological potential of the whole tree is influenced by relations of sources and sinks, which in turn may impair the maintenance of the fruits set.

Endogenous hormones in fruits

The dependence of fruit initiation on seed set in flowering plants suggests that fertilization-dependent pollen and seed-derived signals are required for fruit initiation and subsequent development. For example, localized but unknown signals from seeds influence. Several plant growth regulators such as Auxin, Gibberellins (GAs), and cytokinin perform a vital role in growth and development of both fruits and seeds. Both pollen and developing seeds contain plant hormones, and they may serve as sources of some of these hormones. However, movement of hormones from pollen and seeds directly into fruit progenitor tissues has not, to our knowledge, been demonstrated.

Lewis et al. (1965) reported that fruit set in the parthenocarpic navel orange was found to be correlated with a high level of citrus auxin, a compound distinct from indoleacetic acid. The period of maximum fruit drop coincided with a change in pattern of accumulation of this auxin and the initial detection of an inhibitor. Auxin stimulates the production of ethylene by roots, stems, leaves, and fruits. In Fig the usage of 2,4,5-T was found effective to hasten the growth and maturation as much as 60 days.

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Stimulated by the fact that auxin application promoted ethylene formation and subsequent flowering in pineapple plants (Burg and Burg, 1966).

The low concentration of auxin hormone in flowers and pollen grains resulting of poor pollen tube growth which leads to poor fertilization and fruit set. Application of an auxin will increase the auxin concentration in flowers which cause better growth and development of pollen tube with better fertilization and fruit set. The deficiency of boron in flower parts will excite the performance of the enzyme indole acetic acid (IAA) oxidase. This enzyme grounds the accepted break-down of auxins hormone foremost to lower the auxin levels in floral parts.

Plant Hormones and Fertilization-Independent Fruit Formation

Despite the usual requirement for seed set, the uncoupling of fruit development from the process of fertilization and seed development to produce seedless (parthenocarpic) fruit. (Varoquaux et al., 2002). The genetic basis of seedlessness has been exploited by various field farmers and plant breeders for the production of seedless fruits and elevated endogenous levels of plant growth regulators have been observed during parthenocarpic fruit set, suggested that continuous supply of phytohormones to sink from sources other than pollen and seeds may be satisfactory to induce fruit growth. Parthenocarpy can also be induced in varied agricultural species by the exogenous application of auxins, GA_s and cytokinins.

Transitional Phases -Flowering and Initiation of Fruit and Seed Development

While the physiological basis for seed and fruit initiation and growth has long been attributed to changes in plant hormone levels, the primary hormone cue and the sequence of signal transduction events leading to the coupling of fruit and seed development have remained unresolved. Recent molecular studies on fruit formation due to fertilization-independent in both tomato and Arabidopsis, have identified that the auxin signaling is one of the initial actions in the initiation of fruit cascade. Moreover, the various components of the auxin signaling pathway involved in curbing fruit initiation until the fertilization prompt (Goetz et al., 2006).

Regulation and Manipulation of Flowering and Fruit setting

1. Induction of flowering

Gibberellins generally inhibit flowering with the exception of GA₁ and C-3 epi-GA₄, which have been shown to promote flowering in apple-trees. More than 90 percent flowering is induced in pineapple by the urea (2%) and CaCO₃ (0.04%) after 50 days of application. The flower and fruit number can be increased by spraying the urea @ 1ml/

l due to greater ethylene forming enzyme activity in leaves leading to maximum number of flowers and fruits in guava. Urea has been tried to induce flowers in "off" season in different cultivars of mango but the results obtained were erratic. However, results have indicated that ethylene may promote flowering in mango only when

conditions for bearing are not otherwise unfavorable. In guava foliar application of NAA @ 600 ppm or 10 % urea during the full bloom results in full flower drop in summer and better fruit setting can be obtained in winter for better returns.

2. Remedial measures for inadequate winter chilling

At high altitudes in tropics and sub-tropical and temperate zones, temperatures may be low enough to induce dormancy, but not sufficiently low to satisfy chilling requirements. Foliation is delayed and bud break may extend over longer periods, giving problems in cross-pollination. In Brazil, a combination of 2% thiourea and 10% potassium nitrate, followed by 4% mineral oil and 0.12% DNOC has been approved in Apple. Breeding of low-chilling apple varieties has made it possible to grow apples in warm fruit-growing areas.

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3. Control of blossom quality

In pome and stone-fruits, blossom quality, as measured by fruit-set, when blossoms are pollinated by hand, varies considerably from tree to tree and from one season to next. It can be improved by cultural practices such as branch bending (Robbie and Knight 1985). The physiology behind bending is that it restricts carbohydrate movement and auxin from the upper portion of the limb towards the roots. An accumulation of carbohydrates and slowing down of the growth beyond the bend is, therefore, assumed to be favourable to flower bud formation. High temperatures in early spring, between the completion of rest period and blossom opening, have led to reduced fruit-set and this has been shown to be at last in part due to a shortened duration of ovule viability. Supplementary pollination at blossom time or blossom thinning in a heavy crop year is likely to be beneficial.

4. Control of pollination

In Self- incompatible fruit the pollen transfer is the present application problem. Various cultivars of apple partially self-fertile under warm weather, but in many cases the fruitset improved by the utilization of pollinators such as pollinizing varieties and honey bees. Some stone fruits viz. Cherries and plums also requires cross pollination and these should be interplanted with pollinizing varieties.

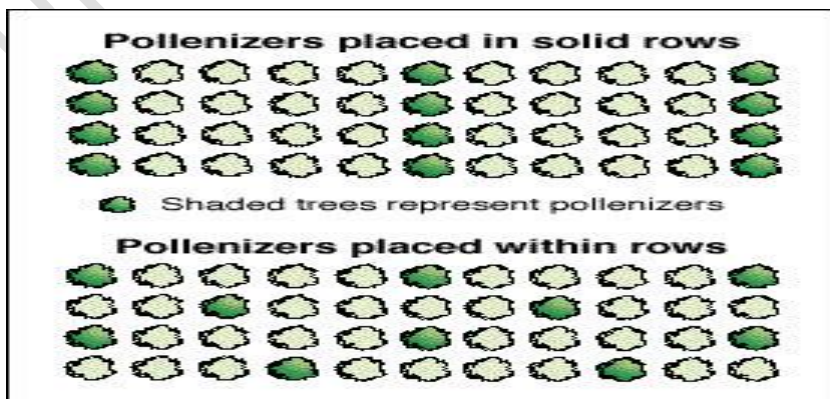
The various techniques of breeding and selection in term of self-fertile cultivars may help to achieve acceptable pollination in cool marginal areas where the temperature duringflowering periodisdesirable for both bee activity and growth of pollen-tube (Alston and Spiegel-Roy, 1985). Until the availability of such improved breeding techniques, the establishment of appropriate pollinizing cultivars and bee-hives can be of great help to ensure satisfactory fruit-set. The increasing tendency for using crab-apples, as a pollinator alsooccupying very little space in orchards so it is worthwhile to use only a number of pollinator varieties with widespread flowering dates to ensure cross-pollination.

The decrease in the number of natural pollinators due to indiscriminate use of chemicals and worsening of ecosystem. Managed bee pollination is very limited and available bee hives during bloom hardly meet 2- 3% of the demand. All these factors have lead to poor fruit setting in Delicious (Gautam et al., 1990).

5. Enhancement and induction of fruit-set and retention

Fruit-set is frequently suboptimal in apple, pear, plum and cherry. This can often be increased by tipping growing shoots to reduce competition from these either just after flowering or at any early fruit let stage.Fruit set can be aided or induced by application plant-growth substances at flowering or after this. Mixture of GA₃ with an auxin induces fruit-set of cherries. GA_{4,7} is generally more effective than GA₃ on apples (Modlibowska, 1975).

Chart 3. Control of pollination



6. Control of frost damage

Fruit-buds become more sensitive to frost towards full-bloom partly as the result of the increase in water content. Even buds at early stages can be de-hardened by a period of warm weather. Breeding for late-flowering varieties should offer effective control (Jones, 1985). Efforts to increase frost hardiness by chemical sprays or to delay blossoming by use of plant-growth regulators have not yet been as successful to be adopted on a large scale.

7. Reduction in crop load

The first approach to reduce number of fruits per tree is by pruning. This usually involves selective removal of thin shoots with weak fruit-buds; which will give small fruits and have less number of spurs. However, thinning fruitlets after blossoming provides a more flexible technique for adjusting actual fruit load in any particular year.

Blossom thinning by DNOC is practical when there is certainly of oversetting in the absence of thinning e.g. Golden Delicious grown in favorable climates and with minimal pruning. It is achieved by physical damage to blossoms, by preventing pollen germination and by inactivating pollen-tubes growing down the styles. Post-blossom thinning of apples is usually achieved by the use of NAA or Carbaryl (sevin). Childers (1983) suggested chemical application between 10 and 25 days after full bloom. NAA application imposes a physiological stress on the tree which causes shedding of least vigorously growing fruitlets. The growth of the remaining fruit may also be checked, their ultimate size may also be less as compared to hand-thinning.

8. Hybridization

Improved technique of hybridization in mango helps to develop hybrids for airof desirable characters. Embryological studies revealed that in mango flowers the pollen tubes nurture downward the style and cause effective fertilization but the progress of zygote is impassable due to saprophytic type of incompatibility. The process of hybridization in large scale provides a resolution to the biennial bearing problem (Mukhjereet al., 1968).

9. Irrigation

Maintenance of proper soil moisture at the time of flowering and fruit set is every important. Excessive soil moisture or water stress during these processes results in flower and fruit drop. It has been reported that the irrigation was stopped at the end of September and trees were stress for 6-weeks until beginning of rains in November-December, it set and doubled the yield of litchi while irrigation at 20% or 40% soil moisture depletion gave maximum fruit set and yield of mango (Chandel and Singh, 1992).

10. Nutrition

Various nutrients such as Nitrogen, Phosphorus, Calcium, Magnesium, Zinc, Potassium and Boron have a specific role in maintaining the fruitful behaviour of the plants. The balance application (through soil and foliar application) and availability of these nutrients is very much essential for obtaining good fruit set and yield. Fruit retention was significantly improved by the application of $ZnSO_4$ in Kinnow (Daultaet al., 1986).

11. Application of Plant Growth Regulators

In several fruit plants the unproductive nature can be overwhelmed with the application of phytohormones. Some of the recent findings on unfruitfulness are given in the following table.

Table 1. Responses of plant growth regulators

Fruit Crop	Growth regulators	Response	Reference
Apple	NAA or Carbaryl (at full	Decrease fruit set Increase	Komzik (2004)

	bloom stage)	yield	
	GA ₃ +NAA(At petal fall)	Increase initiation and final set	Jackson et al., (1983)
	Ethephon (for thinning)	Decrease fruit set Increase size of fruit	Metz (2005)
Lichi	TIBA,KNO ₃	Increase pollen fertility	Sanyal et al.,1996
	NAA,200ppm	Increase size, quality and retain bloom	Cuello et al.,1992
	Baoguoji (to prevent fruit drop)	Increase fruit set Increase photosynthetic rate	Liu et al., (2000)
Grapes	GA ₃	Increase fruit set	Hyatt et al.,1994
	CCC@ 2000 mg/l	Increased fruit set Inhibited shoot growth	Todic (2004)
	CPPU (10 ppm) 14 days after bloom	Increase fruit retention, yield and quality	Notodimedjo (2000)
Citrus	GA ₃	Increase fruit retention	Turnball,1989
	2,4-D@10ppm	Increase fruit retention	Daulta et al 1986
	<u>Paclobutrazol@2.5g/l</u>	Increase fruit set	Walstenholme et al.,1990
	Ethephon	Increase fruit yield	Dumer and Gianfago,1992
Pear	GA ₃ @50ppm	Increase fruit set and retention, Parthenocarp	Yuda et al.,1993
	1-MCP 0.75 µ/l during prepollination	Increase fruit set	Franco et al., (2005)
	GA ₃ 10 g/ha	Increase fruit set	Decker et al., (2000)
Peach	Dormex,Paclobutrazol,KNO ₃	Reduce fruit set`	George and Nissan,1993

Fruit Growth and Development

Fruit is the structure that arises from an ovary (or several ovaries and in some cases associated floral parts) after fertilization and supports the developing seeds. It is an evolutionary adaptation unique to flowering plants and is designed to aid in the dispersal of seeds by various agencies.

Stages of fruit development

In most species, fruit growth can be represented by a sigmoid curve or a double sigmoid curve with a second burst of growth during the ripening period while Kiwi fruit follows a triple sigmoid growth curve. Physiologically and biochemically fruit development can be divided into four phases, which although continuous, are separated on the basis of major activities.

Phase-I: It includes ovary development in the flower, and flowering anthesis, a decision to abort or proceed with further development (i.e. rupture of anther store to release mature pollen).

Phase-II: This phase involves a period of most rapid cell divisions.

Phase-III: It is the period of most rapid growth when cell divisions more or less cease, and growth is almost exclusively by cell enlargement. In this phase, food reserves are accumulated and most fruits attain their final shape and size before the onset of ripening.

Phase-IV: Ripening phase.

In some fruits, such as avocado, cell division may continue well in to phase-III.

Fruitcrop	Periodofcelldivision
RibesandRubus	Celldivisionceasesatanthesis
Cherry	Ceasesabout2weeksafteranthesis
Plum	4weeks
Apple	4-5weeks
Pear	7-9weeks

Sometimesduringcelldivisionperiod,cellenlargementbeginsandproceedsatarapidrate. Atblossomtime,intercellularairspacesareabsentorverysmall. Concurrentwithcellenlargement,airspacesincreasetoamaximum, and then remain constantfortheremainderoftheseason. Earlyinthecellenlargementphase, vacuolesforminthecellsandincreaseinsizeasthecellenlarges,ultimately occupyingmostofthespaceinthecentre. Thecombinedgrowthresultingfromcelldivision,cellenlargementandair spaceformationresultsinageneralsigmoidal(S-shaped)curve. Somefruitssuch asstonefruits-current,pistachioandseededgrapehaveadoublesigmoidal growthcurve. Thefirstslowgrowthperiodofstonefruitscoincideswiththe periodofpithardeningduringwhichlignificationsofendocarp(stone)proceeds rapidlywhilemesocarp(flesh)andseed(kernel)growthissuppressed. Nearthe endofpithardening, fleshcellsenlargerapidlyuntilthefruitisfirmripe, after whichgrowthslowsandstops.

FruitDevelopmentStages

1. Celldivision:

- Predominatesafterbloom.
- Smallerfruitedcropsgenerallyhaveashorterperiodofcelldivision.
- Extendedinsomebyblossomthinning.
- 2millioncellsinfleshofappleatanthesisrequire21 doublingsofcell number.
- 40millioncellsatharvestrequireonly4.5doublings.
- Mostpost-anthesiscelldivisionsoccurinfirstfewweeksafterbloom, butaslong as100days.

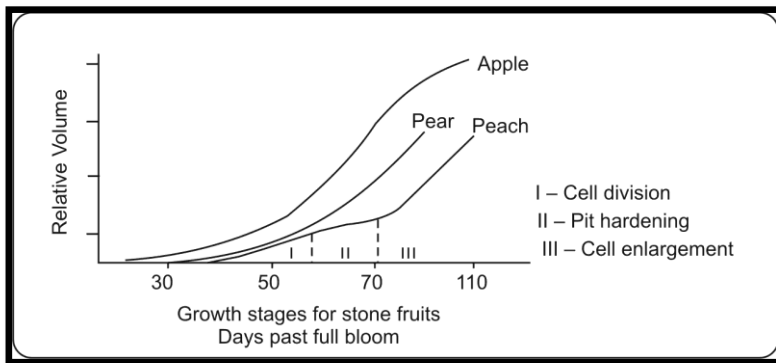
2. Pithardening(stonefruitonly):Lignificationsofendocarp

3. Cellenlargement:

- Predominateslaterinfuitdevelopment(andafterpithardeninginstone fruit)
- Beginssoonafterpollination,continesthroughcelldivisionstage,then at diminishingrateuntilharvest

4. Fruitmaturation: Finalweeks(days)offruitdevelopment

Chart 4.
Relation
ship
between
relative
volume
and days
for full
bloom



(Jackson, 1975)

Key Growth Stages

Dormant: Fruit buds relatively inactive. This is the overwintering stage, (applies to all fruits).

Silvertip: Applies only to apple. Fruit bud scales separated at tip, showing light gray tissue.

Swollen bud: Equivalent to silvertip stage in apple. Fruit buds swollen, scales separated to expose areas of lighter colored tissue (applies to all fruits except apple).

Greentip: Applies only to apple. Fruit buds broken at tip, showing about 1/16 inch (1-2mm) green.

Budburst: Equivalent to greentip stage in apple. Fruit buds broken at tip, showing tips of blossom buds (applies to pear, sweet and tart cherry, plum and prune).

Half-inch green: (centimeter green): Applies only to apple and peach. In apple, when about 1/2 inch (1cm) of leaf tissue is projecting from the fruit buds. In peach, when the leaf bud occurring between a pair of fruit buds has produced about 1 cm of new growth.

Tight cluster: Applies only to apple. Blossom buds mostly exposed, tightly grouped, stems short.

Green cluster: Applies only to pear, plum and prune. Blossom buds green, mostly separated in the cluster, stems lengthened.

Pink: Applies only to apple and peach. For apple, all blossom buds in cluster pink, stems fully extended. For peach, when the blossom bud shows a pink tip.

White bud: Applies to pear, sweet and tart cherry, plum and prune. Blossom buds white, separated in the cluster and stems lengthened.

Bloom: Blossom buds open (applies to all fruits).

Petal fall: After about 75 percent of the petals have fallen (applies to all fruits).

Fruit set: A stage ranging from about 4 (cherry) to 10 (peach) days after bloom when the blossoms that have or have not set fruit, initially, are clearly evident (applies to all fruits).

Factors Affecting Fruit Growth and Development

1. Effect of hormones: Auxin, GA and cytokinins are involved in the early stages of fruit growth, especially in Phase-I and Phase-II, although their exact roles and interrelations among them are unclear. In Phase-I, sources

of hormones is material tissues, but in Phase-II and III, which coincides with embryo growth and maturation, respectively, the source of hormones is debatable. The hormones could be synthesized *in situ* or translocated from other parts of the plant via the phloem stream. There are also instances where fruit growth is affected by auxins and/or CKs produced by the embryo and endosperm.

Role of auxins: The influences of seed on fruit growth were shown by Nitsch (1950) in strawberry. It is an aggregate fruit. A fruit formed from several single carpels in a flower. Each carpel has a single seed and produces an achene (a joint structure of seed and the surrounding ovary wall). Achenes are borne on the receptacle, which form the fleshy fruit. Nitsch removed varying numbers of developing achenes from young fruit of strawberries and showed a strong correlation between the number of achenes left and the fruit growth around them. Similar positive correlations between the number of seeds and fruit growth have been shown for other fruits (e.g. grapes, blackberry, apple etc.).

In addition to auxin, CKs and GAs also play a role in the growth of the young fruit. Cytokinin levels specially zeatin and zeatin riboside are high at the earliest stage of several fruits and correlated with period of maximum cell division. In kiwi fruit, the concentration of total cytokinins was high at the earliest time after anthesis, dropped to low levels later (Lewis *et al.* 1996).

2. Fruit size and shape: The shape and size depend on the number of cell divisions and directionality of growth of daughter cell in various sectors of fruit in phase II and III. The growth of banana requires cell growth mostly in a longitudinal direction and growth of pear fruit would be required altered patterns of cell division and growth in different sectors of the fruits.

3. Leaf ratio: Leaf ratio plays an important role in fruit growth and development. It varies from crop to crop. 30-40 leaves are considered optimum for apple.

4. Photoassimilates: During the rapid growth in Phase II and III, fruits act as strong sink and import massive amount of photoassimilates from photosynthesizing organ. Such translocation occurs in the phloem tissue and the translocated materials are mostly sucrose, although in some species oligosaccharides (raffinose) or hexitols (mannitol, sorbitol) may be the predominant sugar/sugar alcohol. Hormones have been implicated in regulating the partitioning of photoassimilates between competing sink. In many studies, ABA has been suggested as the hormone that facilitates unloading of the photoassimilates at the sink site, but evidence is equivocal.

Fruit development in some important fruits

Mango

The flowering period in mango is usually of two to three weeks. It is achieved by low temperature, whereas high temperatures shorten it. It bears mainly two types of flowers—

male and perfect, though neutral flowers are also found occasionally. The percentage of perfect flowers varies and is influenced by the environment in which these are grown. During the period of panicle development, low temperature increases proportion of male flowers. The fruit set is directly related to proportion of perfect flowers initially but final retention appears to be genetic characteristic of the cultivar. The initial fruit set in Langra is very high, but ultimately retention per panicle is better in Dashehari which has a relatively lower proportion of perfect flower (Majumder and Sharma, 1996). The fruit growth followed a sigmoid pattern and in general, growth is rapid between 30 to 90 days after fruit set. The fruit volume is initially more than that of fruit weight and the difference of fruit

volume and weight is narrow upto 70 days after fruit set. Afterwards, the fruit weight was greater than that of the volume. With the advancement of maturity the number of lentils decreases. The mango seed also follows a sigmoid growth. The rapid increase in length and diameter of seed was recorded upto 60 days after fruit set (Dutta and Dhua, 2004).

Citrus

Citrus species usually produce a large number of flowers over the year. The floral load depends on the cultivar, tree age and environmental conditions (Monselise, 1986). It has been reported, for example, that sweet oranges (*Citrus sinensis*) may develop 250,000 flowers per tree in a bloom season although only a small amount of these flowers (usually less than 1%) becomes mature fruit. Thus, flowering represents a great input for citrus trees and to some extent even a waste of resources. For some authors, however, this reproductive pattern may be linked to a survival strategy. Under unfavorable environmental conditions, such as late frost or drought or excessive rain etc. most of the citrus species produce poor fruit set and high fruit drop results in poor yield.

Grapes

Pollination, fertilization and seed development results in berry set. However, some cultivars set by parthenocarpy. In seedless cultivars, fertilization occurs but the embryo subsequently aborts which is termed as stenospermocarpy. The grape berry growth follows a double sigmoid growth. Berry growth and development in Pusa Urvashi observed a double sigmoid growth pattern like those in typical seedless grape genotypes; however, the total duration was remarkably short including lag phase. Vines were trunk girdled at fruit set stage alone or in combination with three concentrations of GA₃ (20, 30 and 40 ppm) once and twice after a week of first application to improve berry quality. The different combinations of girdling and GA₃ showed that trunk girdling at fruit set prior to application of 40 ppm GA₃ at full bloom hastened the berry ripening by 5 days. Berry quality improved without affecting the yield, i.e. by loosening the bunch with uniform, large and elongated berries having better TSS/acidity ratio.

Apple

Due to lack of cultivar suitable for cross pollination fruit set of apple may be affected. Weather conditions during blooming season, such as temperature, rain fall and humidity may also produce an unsatisfactory fruit set. Frost at bloom time can prevent pollination by killing the style. High relative humidity (>50%) in March, delay flowering without affecting fruit set and yield. Very low temperature (<4.5°C) reduced fruit set by interfering pollener germination and bee activity. Spray of aminoethoxyvinylglycine (AVG 200 ppm) applied alone or with GA + BA (50 ppm) inhibits endogenous ethylene production and increase fruit set in treated flowers (Greene, 1980). There is a continued enlargement of receptacle during the development of fruit. A rapid phase of cell division occurs in first few weeks after pollination, which ceases abruptly 30-40 days after full bloom in Cox's Orange Pippin. The subsequent fruit growth occurs mainly due to cell expansion. The fruit growth pattern follows a smooth sigmoid curve (Mitra, 1991). Prebloom applications of GA₃ at 10 ppm + BA at 5 ppm + NAA at 5 ppm gave the best quality fruits (in terms of firmness, total soluble solids and total sugars), and the most efficient in marginal apple growing areas of Himachal Pradesh. 50 percent GA₄+7+50 percent 6-benzyladenine (BA): Promalin stimulates growth of apical portion of apple fruit, increased length/diameter ratio. 5 percent GA₄+7+95 percent BA: Accel, a post bloom thinner that sometimes increases fruit growth (size) of apple.

Gibberellic acid (GA₃):

ProGibb delays maturity and increases fruit

size, soluble solids and firmness of cherry fruit.

CPPU and BA: Crop load reduction with commercial thinners is used to increase fruit size. Although, total yield is reduced, the remaining fruits are of high value because of their increased size. Benzyladenine (BA) is used to thin apples and it increases fruit size (Moran and Southwick, 2000) by stimulating additional cell divisions within the fruit (Wismer *et al.*; 1995). CPPU [N(2-chloro-4-pyridyl); N-phenylurea] at 10 ppm and BA (Benzyladenine) at 50 ppm resulted in significant increase (>50%) in fruit size of Royal Gala cv. of apple when applied two weeks after full bloom due to stimulation of fruit cortex cell division. BA promotes

cell division in tissues possibly by increasing zeatin riboside levels in the fruits. Both cytokinins increased fruit size without affecting fruit shape and seed number, and with no reduction in the return bloom or yield of the following year.

Promalin: Promalin (GA+BA) sprayed at 50 percent full bloom and repeated at full bloom in single and split dose to Starking Delicious apple increased the TSS, total sugars, soluble proteins and anthocyanin and decreased acidity. In areas exposed to warm weather during flowering and development promalin treatments improved the quantitative as well as qualitative parameters.

Pear and Stone Fruits

Cross-pollination is required in most of the commercial cultivars of Japanese pear (*Pyrus pyrifolia* Nakai), to set fruits because they exhibit gametophytic self incompatibility. To improve fruit set and produce acceptable commercial fruit size and perfectly round shape, artificial pollination using compatible pollen is common practice in the predominant Japanese pear. Generally fruit set is not a problem in commercial pear cultivars. Fruits of Pathar makhpeer take 150 days to mature and physiological development involves measuring changes in size, specific gravity (SG), skin colour, pigment, TSS, phenolic contents, and fruit firmness. Fruit growth shows 3 phases, active, very active and very slow, as measured by size (length and diameter) and weight. Fruit firmness decreases during the final 50 days to harvest. TSS shows a continuous increase during development (from 7.80 to 13.53%); this increase is most rapid between 15 and 30 days, and again between 75 and 90 days. Reducing and total sugars both increase continuously until harvest and the increases are rapid during 120 to 150 days. (Mann and Singh, 1990).

Plum

All *Prunus* species follow the double sigmoid growth curve. During the subsequent development of the fruit the outer wall of the ovary gives rise to three distinct layers of the pit. Two hypodermis layers in the ovary produce the skin of the fruit, which consist of cuticle, the epidermis and a few layers of collenchymatous cells. The flesh contains most of the vascular bundle of the fruit, which are embedded in the lignified tissue of the pit. The fresh fruit weight and size increases throughout the growing season, while the sugar content increases gradually and rapidly during ripening. Dry matter content increases gradually, being sharper at ripening. The organic acid increases initially but decreases during fruit development (Josani and Chohan, 1982).

Strawberry

Maximum fruits in strawberry develop from tertiary flower than from primary and secondary flowers. Plant growth, development and composition of fruits are affected by genetic factors. However, environmental factors such as

water availability, day and night temperature and daylight intensity also influence the fruit production. The effects of temperature as well as its interaction with other environmental factors, like photoperiod often vary with cultivars and species. The influences of day/night temperature combination on plant growth and fruit quality was studied by Shiow et al. (2000) in cv. Earlighlow and Kent of strawberry. The optimum day/night temperature for fruits was found to be 18/12°C.

Loquat

Loquat trees flower profusely in compressed panicles, and although fruit set percentage is very low, fruit size is commonly very small. In fruit crops, fruit size is inversely related with number of fruits produced per tree. Increase in average fruit size can be obtained by thinning the fruit manually or chemically or by applying synthetic auxins at the onset of cell enlargement (Agusti et al., 2005).

Regulation and manipulation of Fruit development

1. Climatic factors : Climatic factors like late spring frosts, precipitation, rainy days and low noon temperatures produce most negative effects on percentage fruit set and yield. Unfavourable meteorological conditions during flowering produce low yields and the greatest reduction in yield has been found to be due to late spring frosts (Grabowsky and Zielenkiewicz, 2000).

2. Chemicals : Dormex spray resulted in earlier flowering by 2-5 days in apricots and plums by 4-8 days. Application of 1 per cent and 2 per cent hydrogen cyanamide (Dormex, 49%) gave better flower and vegetative bud break ratio, fruit set and fruit development in dormant trees of Papaz plum and Tokaloglu and Karacabey apricot cultivars. The highest bud break and fruit set ratios were 87.67 and 85.33 per cent in Papaz plum treated with 2 per cent hydrogen cyanamide, respectively. Promalin applications also caused better flower and vegetative bud break, fruit set and effect fruit yield. Chemically treated trees could be harvested 2-9 days earlier than control trees. Spraying with PCPA (4-CPA) at 30×10^{-6} M at the stage of 75 per cent flower fall increased the fruit set and hence effect fruit development. Application of mixture of 30×10^{-6} M PCPA + 2000×10^{-6} M borax + 2000×10^{-6} M potassium dihydrogen phosphate also produced good effect on fruit size and quality (Wu *et al.*: 1993). Dipping of berries of grapes in GA @40 ppm when berry size is 4mm and again after a week along with girdling of vine resulted in improve size of berry in grapes.

3. Water stress: Growth of shoots, flowers and fruits in deciduous trees appears at different times and therefore the timing of regulated deficit irrigation can influence its effects. The stage II of fruit growth has been identified, as an appropriate period at which fruit growth is minimal and therefore not affected by drought, while shoot growth can be reduced in stone fruits. In early cultivars, this period is very short, the main shoot growth occurs after harvest, and thus may be ideal time for droughting (Johnson and Handley, 2000). It was reported that, water deficit during fruit growth reduced average fruit weight, with a negative correlation between fruit size and integrated mid day stem water potential. In contrast, drought after harvest did not affect flowering, fruit set, fruit growth or yield, in the short term, but drought may reduce productivity, in the long term, as a consequence of the cumulative effects of water deficit on tree growth. Regular irrigation during critical period i.e end March to End April in early cv. Partap, Florida Prince and end April to mid May in late cv. under subtropical condition resulted in higher fruit weight and quality in peaches.

4. Nutrients: The tree performance (branch elongation, flowering and fruit setting intensities) and fruit size has been found to be increased by titanium sprays in combinations

Comment [R13]: Geographical location maybe indicated

with other commercial compounds containing Ca²⁺ and Mg²⁺. This improvement due to calcium absorption as a consequence of the beneficial effect of titanium is on the absorption, translocation and assimilation processes (Alcaraz *et al.*; 2003).

Fruit Drop/Abscission

The most important components of fruit drop are: the rootstock, the combination of polliniser varieties, the conditions depending of nutrition, the extent and timing of the administration of fertilizers, the moments of water stress and the timing of agro-technical interventions. Further adversities may appear as flushes of heat and drought, the rainy spring weather during the blooming period as well as the excessive hot, cool or windy weather impairing pollination, moreover, the appearance of diseases and pests all influence the fate of flowers of growing and become ripe fruits. As generally maintained, dry springs are causing severe fruit drop. In analysing the endogenous and environmental causes of drop of the generative organs (flowers and fruits), the model of leaf abscission has been used, as a study of the excised, well defined abscission zone (AZ) seemed to be an adequate approach to the question. Comparing the effects active in the abscission of fruit with those of the excised leaf stem differences are observed as well as analogies between the anatomy and the accumulation of ethylene in the respective abscission tissues.

Fruit set percentage and severity of fruit drop vary considerably among the major fruit crops. Fruit set may be as high as 90% for blueberries, 10- 20% for apples and peaches to a low of 1% for sweet oranges. Moreover, blueberries have a small percentage of fruit drop after the initial fruit set period, while apples, peaches and citrus have a pronounced and sometimes extensive June drop. The severity of post-bloom drop is a function of cultivar, environment, and cultural practices. Nevertheless, some degree of fruit drop is not only desirable, but necessary. For example, a mature navel orange tree may produce 100,000 flowers. If even 10% of these produced mature fruit, yields would average about 125 boxes/tree.

Abscission (from the Latin *ab* meaning away and *scindere* meaning to cut) is the shedding of a body part. It takes place primarily at predestined sites that are commonly located at the base of an organ such as a leaf, flower, fruit or seed. Trees shed many parts besides leaves, including fruit, flowers, bud scales, trichomes, abscission twigs, and bark.

Fruit drop may be divided into 3 major periods for citrus.

Post bloom Drop

Post-bloom drop occurs during and within a few weeks of bloom, involving the abscission of flowers and small fruit. Post-bloom fruit drop accounts for an 80-90% reduction in the total flower number. The causes of post-bloom drop include inadequate pollination, water or temperature stress, inadequate nitrogen levels, and natural abscission probably regulated by hormone imbalances in the fruit.

June drop

June drop is a common occurrence for many fruit crops. As the name implies, June drop occurs in June for many temperate crops, like apples and peaches. Fruit size generally ranges from 1 to 3 cm in diameter during this time. June drop is most severe and troublesome to growers in arid climates where temperatures routinely reach 40°C. Although many causes have been proposed for June drop including water stress, hormone imbalances and competition among fruitlets but high temperature stress appears to be the most important cause.

Pre-harvest drop

It is the most serious fruit drop which resulted in the higher economic loss to the grower and it is very difficult to control. It occurs after the fruit have reached legal maturity but prior to harvest. The problem is most severe for 'Temples', 'Pineapple' oranges, and 'Murcotts'. but also is a problem for navel 'Minneolas' and grapefruit when held on the tree

Comment [R14]: Comparison and discussion should be more specified for fruits

late into the season Pre-harvest drop used in this sense is not caused by a specific organism or environmental factor but is simply due to natural aging and abscission.

Changes during fruit drop/abscission

During abscission changes occur at morphological, anatomical and biochemical levels.

Morphological and Anatomical Changes

1. Formation of abscission zone at the junction of abscising organs (flower, fruit) and the parent plant body.
2. Swelling or constriction of abscission zones w.r. to the parts of pedicle.
3. Abscission zone is 1-2 rows or up to 15 or more cell tier thickness.
4. Cells are parenchymatous, devoid of lignin and suberin, dense protoplasm, more starch, small intercellular spaces and highly branched plasmodesmata.
5. Stele usually divides into separate bundles before it enters the zone.
6. Dissolution of middle lamella resulting in loosening of cells.
7. Weakening and breaking of vascular connections between leaves, fruits, flowers and the parent plant.
8. Development of periderm to protect the exposed surface and cells become suberised.
9. Formation of tyloses (bladder like protrusions from xylem parenchyma cells) which block xylem vessels.

Biochemical changes

1. Enhanced production of hydrolytic enzymes - cellulase, pectic enzymes, lignase which caused dissolution of middle lamella and primary wall of the cells in abscission zone.
2. Polygalactouranase leading to breakdown of middle lamella.
3. Capectate in middle lamella is hydrolysed to pectic acid and pectate.
4. Cell expansion by cellulase in abscission zone.
5. Hydrolysis of lignin by lignases.
6. Auxin destruction by increased peroxidase activity.
7. Active synthesis of proteins and RNA in abscission zone.

Beside the above changes, many other processes take place to prepare the plant for this event. For instance, the vascular elements that service the organ are occluded and the exposed fracture surfaces are protected from water loss and invasion by pathogens.

Abscission zones

Abscission zones occur at the base of fruit pedicle and at the base of leaflets. Fruits are shed through a number of biological actions which weaken cell walls and initiate cell tearing away from one another. Abscission zone cells tend to be smaller, more densely packed, with no intercellular spaces, less lignin, and have remained in a cell division phase longer than surrounding cells. Additional cell divisions in this zone prepare these cells for later abscission processes. In most abscission zones, there is a single fault line which develops and is accentuated by additional wall degradations. Cells adjacent to fault line cells will have weakened walls also, allowing any fracture to propagate along several paths for short distances.

Wall weakening: The abscission process begins with growth regulator signals initiating cellular changes. Abscission zone cells secrete pectinase and cellulase (wall degradation enzymes). These enzymes degrade the strength of the middle lamella and primary wall between cells. The middle lamella, the glue which holds cells together, begins to dissolve in the abscission zone. At the same time,

surrounding primary walls begin to swell from changes in chemical components. **Wall changes:** As cell wall interconnections are weakened, water pressure within thin-walled cells (turgor pressure in parenchyma) causes these cells to expand. As cells expand, they generate shear forces by pushing and pulling on surrounding weakened walls. Mechanically, fracture lines begin to develop between cell walls. As cell walls pull apart from one another, this open wound is being closed by deposition of blocking materials and protective compounds. A strong protective boundary zone is prepared to defend remaining tree tissues from the environment and pests. Tyloses, suberin, lignin and other protective boundary setting materials are developed and deposited on the tree side of the abscission zone.

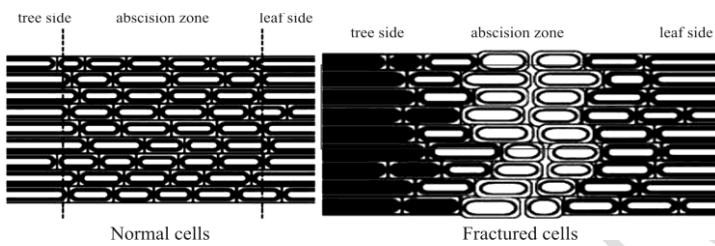
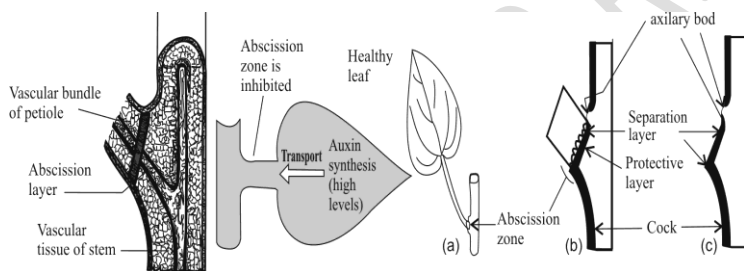


Fig 1: Two-dimensional diagram showing cells in a leaf base abscission zone with a fracture line between cells. Tree protection zone, wall degradation areas, and cell expansion zone all disrupting cell-to-cell connections are clearly shown.



(www.answers.com/topic/abscission).

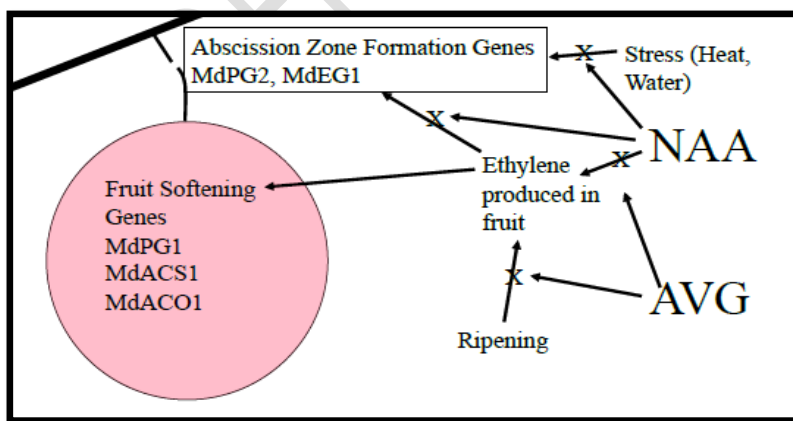


Fig.2. Proposed Model of Abscission (Rongcai Yuan, 2008)

Regulation of Fruit drop

Comment [R15]: Trends, new perspectives, gaps, conflicts, or problem(s) maybe indicated

Auxin is a primary growth regulator produced in the fruit and slowly transported towards the stem base through living cells. As long as auxin is effectively being transported across the abscission zone, abscission zone cells remain unresponsive. As auxin production begins to decrease in fall and auxin transport rates begin to decline due to less auxin availability, damage to living cells transporting auxin, and/or accelerating infection of living tissues by pests, cell wall changes are initiated. Cell wall changes increasingly inhibit auxin transport and accelerate ethylene production. Small amounts of ethylene hasten abscission zone development. Abscisic acid is responsible (in part) for dormancy onset in the leaf and stimulates ethylene production and inhibits auxin transport. During abscission endogenous auxin and cytokinin content decrease sharply while ABA and ethylene increase.

1. Regulation of timing: The time from the differentiation of the abscission zone to organ shedding can range from days (or even hours) to many months. It is well documented that the main abscission accelerating agent is ethylene while the plant hormone indoleacetic acid (IAA) delays the process. It has been proposed that by altering the balance between these two naturally occurring stimuli the timing of abscission can be accurately controlled in plants. The origin of the elevated ethylene that precedes organ shedding emanates from tissues distal to the AZ such as the diseased or senescing leaf blade, or ripening fruit in climacteric species. Although application of ethylene has been shown to promote abscission, floral organs of *Arabidopsis* mutants such as *etr1*, that are blind or insensitive to the gas, are shed at a later stage of development than wild type indicating that it is not an absolute requirement for shedding to be initiated (Patterson, 2001).

2. Regulation of cell separation: Abscission leads to a series of events that result in cell separation at the point of organ detachment. Ultrastructural analysis indicates that this is primarily a consequence of the dissolution of the middle lamella and that immediately prior to shedding it is only the lignified tissues of the vascular trace that retain an attachment to the parent plant. These connections are thought to be finally severed by the hydraulic expansion of the isodiametric AZ cells once the constraints imposed by the matrix have been loosened. A number of mechanisms have been suggested that bring about wall breakdown but most important is by an enzymatic process (Sexton and Roberts, 1982).

3. Protection of fractured part: Once cell separation has taken place and the subtending organ has been shed, the scar remaining provides an ideal site for invasion by bacteria and fungi. But the remaining cells divide and suberize to protect the wound. The broken xylem vessels become blocked with gums or tyloses and the phloem sieve plates are callused over to prevent pathogen entry.

Manipulation of fruit drop

Too little abscission of young fruits results in production of large number of unmarketable fruits where as too much abscission results in uneconomical yields. Hence manipulation of abscission under certain conditions is desirable. There are different techniques through which abscission can be manipulated. Broadly they can be categorized as follows:

- 1. Understanding physiological basis of abscission:** By understanding the physiology of abscission, flower and fruit drop can be manipulated accordingly.
- 2. Genetics of abscission:** Breeding of varieties with different abscission characteristics for example raspberry cultivars. There are two types of cultivars viz. hand picking ones that do not drop ripe berries by shaking the bush and mechanical picking types, where fruit easily detach.
- 3. rDNA technology:** Use of antisense RNA technology for ACC synthase to

block the ethylene synthesis and hence slowing abscission. It is also used for wall degrading enzymes cellulase and polygalactourase (PG).

4. **Acceleration of abscission:** By increasing ethylene production. e.g. spraying ethephon, wounding.
5. **Inhibition of abscission:** Reducing ethylene production or interfering with ethylene action. e.g. use of antagonists like AVG, AOA, silver thiosulphate, DACP.
6. **Prevention of abscission:** Use of auxins and cytokinins

Fruit drop in some fruit crops

Citrus

The most pronounced stages of fruit drop are, (i) immediately after fruit set at marble stage which lasts for a month after full bloom, referred as post-set drop, (ii) the second wave of intense fruit drop occurs at the onset of hot summer weather during May-June, known as June drop, and (iii) preharvest drop or premature drop occurring during ripening period, which lasts from August to December-January. Higher summer temperature, excess or deficiency of soil moisture, lack of nutrients like zinc, phosphorus and potash and attack of fungal diseases like anthracnose, stem-end rot and stem-end rot are some of the primary factors responsible for fruit drop. Spray of 2,4-D @ 5 g + Bavistin 50 WP @ 500 g (or Propiconazole 25 EC @ 500 ml) in 500 litres of water/acre in Mid April, August and first week of Sept. along with sprays of Bavistin 50 WP @ 500 g (or Propiconazole 25 EC @ 500 ml) in 500 litres of water in End July and end Sept. If there are broad leaf crops grown nearby, then use GA @ 20 ppm instead of 2-4 D.

Mango

In mango, there is a heavy drop of hermaphrodite flowers and young fruits amounting to 99% or more. In general, in mango 0.1% or less hermaphrodite flowers develop fruits to maturity. The maximum drop of fruits in 'Langra' and 'Dashehari' takes place in the first three weeks of April and differs significantly from the drops in the following weeks. Fruit drop is to some extent associated with the variety, as the variety 'Langra' is more prone to fruit drop than 'Dashehari'. The embryo in the initial stages of its development may yet be another cause of drop. This occurs invariably, if the flowers are self-pollinated. 2,4-D produced better results at concentrations below 20 ppm, because at higher concentrations fruit and seed development is retarded. Spray of 2,4-D @ 20 ppm in end April in Dashehari and in first week of May in Langra produced better results.

Apples

All apple varieties show some fruit drop as they progress through the ripening period but some varieties begin to drop large numbers of fruits early in the ripening period before they develop sufficient red color to meet market requirements. McIntosh is particularly prone to pre-harvest fruit drop. In some years losses can exceed 50% of the crop and frequently pre-harvest drop results in severe economic losses. Application of NAA, diaminozide (alar) and Aminoethoxyvinylglycine (AVG) proved better results in controlling pre-harvest fruit drops.

Stone fruits

Various peach and apricot cultivars showed early and more uniform maturation and improved fruit colour following sprays of 2, 4, 5- TP, SADH or CEPA, but these effects were often accompanied by un-desirable responses such as softening, cessation of growth, or abscission. Other substances, such as chlormequat, ABA and calcium nitrate delayed fruit maturation and increased firmness, whilst phenoxy auxins decreased fruit drop of peach and almond. The use of such compounds, together or in succession, offers possibilities for the

Comment [R16]: Environmental causes of fruit drop might be indicated properly

Comment [R17]: Relevant references might be introduced

practical control of stone fruit maturation. On the almond cv. 'Ne Plus Ultra' good control of pre-harvest drop was obtained with both 2, 4, 5-TP and 2, 4, 5-T when applied about 5 weeks before harvest - the stage when the abscission layer markedly began to develop. Earlier or later sprays were less effective, the latter sometimes increasing the rate of abscission.

Conclusion

Flower bud development involves the transformation of the vegetative apex to a reproductive structure. Three events occur during the transition of bud to flowering i.e. induction, evocation and initiation.

First visible sign of differentiation is when the flat apical meristem becomes domed, then the central meristem is partitioned and the pith meristem develops. Flowers and pollen grains with low auxin levels have poor pollen tube growth, leading to poor fertilization and fruit set. Application of an auxin dominant will increase auxin levels in flowers resulting in better pollen tube development and growth, with better fertilization and fruit set. Correction of Boron deficiency levels will inhibit IAA oxidase and prevent the break-down of auxins present in floral parts

Most fruits follow a sigmoid, some double while some other triple sigmoid (Kiwi) growth curve. Cell division, cell enlargement and maturation are important steps of fruit growth and development. Various internal factors like hormones, cell size, cell number, seeds, photoassimilate etc. and external factors including temperature, light, chemicals, cultural practices etc. influence fruit growth and development. Growth regulators play an important role in development of fruits. Various physico-chemical changes like increase in size, weight, volume, change in colour, TSS, acidity, reducing sugar etc. occur during fruit growth and development.

Fruit drop or abscission is a highly coordinated process that leads to shedding of fruits in plants. Various morphological, anatomical and biochemical changes take place during this process. During abscission there is degradation of middle lamella of cells and formation of abscission zones, and enzymes such as EGs and PGs are thought to play an important role in these events. There is protection of fractured surfaces through expression of PR related proteins. Although many hypotheses have been put forth to explain the process of abscission but the molecular mechanisms remain still unclear.

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Comment [R18]: Make sure to have a clear take home message that integrates the points discussed in the review.

Comment [R19]: Reference list should be rechecked in accordance with the narrative text

Comment [R20]: DOI maybe added

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Comment [R21]: Specific referencing style should be followed

Comment [R22]: should be checked