

Review Article

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Physiology of Flowering in Apple and Almond: A Review

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ABSTRACT

Flower bud formation is a intricate phenomenon. Numerous studies on flower bud formation of temperate fruit plants have been conducted in many .In spite of that, a great part of the most important characteristics of flower bud formation remains insufficiently clarified both by theoretical biology and applied horticulture. Special attention deserves the clarification of the morphogenetic changes that occur between the vegetative state of the buds and the initiation of flower organs. Flowering takes place by the transformation of vegetative apex into a reproductive structure under the control of endogenous and exogenous elements. When the apex of the vegetative bud receives a signal for differentiating as a flower bud, a sequence of events takes place. The mitotic activity increases in the central meristem of apex changing its histological structure. Pome fruits and nut crops start their flower bud development during the previous season and flowers in next spring. In apple initiation generally starts with the ceasation of shoot growth and in almond it coincides with the hull split stage of current crop. The different stages of flower bud development in almond includes bud scales, increase in meristem size, broad dome, initiation of sepal and petal primordia, initiation of stamen and carpel primordia. Large number of factors that influence the proportion of buds giving rise to flowers have generally been interpreted in terms of an in-built propensity to flowering and interference with the attainment of this. Warm temperature advances the flower bud differentiation in apple. Thus understanding the processes of flower induction and flower bud development are important for a lot of horticultural activities particularly in fruit cultivation.

Keywords

Flower bud,
Morphogenetic
changes, Induction,
Differentiation

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Introduction

Plants assimilate environmental cues for their growth and flowering phenomena. In the flowering process, floral transition is the most important phenomena that is regulated by environmental factors. The vital first step for the reproductive phase which determines the blossom intensity and yield capacity is the

differentiation of vegetative primordia to reproductive primordia. The perennial fruit crops are constantly exposed to annual climate variability and climate change and hence, assume greater significance in determining productivity. It is now evident that the different environmental signals influence the flowering time/flowering control such as photoperiod, light quality,

vernalization and other environmental factors like ambient temperature besides nutrient status and moisture stress (Sreekumar *et al.*, 2014).

Physiology of flowering

Plants come to flower after a certain period of vegetative growth. The process until plants come to flower is classified into three stages:

Differentiation of flower buds.
Development of flower buds.
Opening of flower.

The differentiation of flower buds is the most important turning point in this process, and the plant's life cycle switches from vegetative growth to reproductive growth. This switching is called as flowering. Process of flowering involves two steps:

Events in the bud leading to flowering

Three events were proposed to occur during the transition of buds to flowering i.e. induction, evocation and initiation (Metzger, 1987).

Induction: The step at which the flowering stimulus is generated is called floral induction. Searle, (1965) defined induction and induced state as a physiological condition initiated in tissues by external influence such as photoperiod, water stress, chilling temperature, progressively towards flower expression even under subsequent non-initiating conditions.

Evocations: The step at which the shoot apical meristem has received the floral stimulus, and is irreversibly committed to form flower bud primordial is called floral evocation, so these are those processes occurring in the apex essential for the formation of floral primordia (Metzger, 1987).

Initiation: In this process the evoked bud becomes recognizable as a flower bud and is thus committed to reproductive development. This evident the broadening and flattening of the growing point with concurrently developing lobes.

Differentiation of the growing points

The transition from vegetative to reproductive development is marked by an increase in the frequency of cell division within the central zone of the shoot apical meristems. This leads to increase in size of the meristem and shoot meristem is induced to develop sepals, petals, stamens and carpels in place of leaves. The first detectable change in the growing point of the bud after induction of flowering is increasing synthesis of DNA and RNA (Faust, 1989). In temperate fruits, normally 8-14 days are required from the beginning of histological differentiation to the appearance of lower meristem. The first visible sign of differentiation is when the flat apical meristem becomes domed, then the central meristem is partitioned and the pith meristem develops. The stage of flower bud development at any given time during summer and autumn varies with types of bud (basal, middle, upper or terminal shoot buds) and with species and cultivars (Crabbe, 1984).

Environmental signals influencing flowering

Photoperiodism

Relative length of daily light and dark periods helps in transforming a vegetative shoot meristem to a floral bud. The induction of flowering in response to the relative length of daily light and dark period is called photoperiodism. It simply means the duration of light. It is a physiological response of plants in relation to duration of light. Based on photoperiodic responses plants maybe classified into three groups:

Short day plants (SDP)

These plants flower only when exposed to day lengths shorter than a certain critical maximum. Critical day length is 11-15 hours. Most of the plants in tropics are short day plants e.g. pineapple, strawberry etc.

Long day plants (LDP)

These plants begin flowering when exposed day lengths longer than certain critical minimum. Below the critical period, these plants continue their vegetative growth. Most of the temperate zone fruits are long day plants. Critical day length lies between 12-14 hours. Example: Apple, Passion fruit etc.

Day neutral plants (DNP)

These plants flower after a period of vegetative growth regardless of the photoperiod. Flowering is not affected by day length and any time during the year e.g. guava, papaya, citrus, banana etc. (Verma, 2008).

Plants perceive the length of day and night with the help of a protein called as phytochrome. Phytochrome is a homodimer: two identical protein molecules each conjugated to a light absorbing molecule (compare rhodopsin). Plants make five phytochromes: Phy A Phy B, as well as C, D and E.

There is some redundancy in function of the different phytochromes but there also seem to be functions that are unique to one or another. Phytochrome exist in two inter convertible forms: PR because it absorbs red (R; 660 nm) light and PFR because it absorbs far red (FR; 730nm) light. Butler *et al.*, (1959) discovered phytochrome which is widely distributed in green plants and is present within plasma membrane of cells.

Vernalization

Induction of flowering by low temperature is referred as vernalization.

Site of vernalization: Active apical meristem and young leaves.

Hypothesis of vernalization

Chailakhyan's hypothesis: This hypothesis assumes that flowering hormone- florigen is a complex of two types of substances gibberellin and anthesins. Gibberellin is essential for growth of the plant stems and anthesins are required for flower formation. According to chailakhyan (1937), vernalin is produced in plants at low temperature. In long day conditions it is converted to gibberellin. Anthesin is present in long day plants. Anthesin along with vernalin cause flowering in long day plants. But in short day conditions, the vernalin is converted to gibberellin, hence flowering does not occur. Addition of gibberellin to long day unvernallized plants in long day conditions leads to flower formation as these plants contain anthesin. Gibberellin is ineffective in producing flowers in short day plants as they lack anthesin. As postulated by Purvis (1961) the formation of a substance 'A' from its precursor. 'A' is then converted to 'B' after chilling. The substance 'B' is unstable. At suitable temperature, 'B' is converted to 'D' called Vernalin. At correct photoperiod vernalin is converted to substance 'F' (florigen) – a flowering hormone. Florigen induces flower formation proper photoperiod.

Many temperate fruit plants have to go through wintering to flower in the next season and requires cold treatment for the plant to flower. It has been reported that these plants, contain specific proteins and its associated components which bind to loci that are involved in flower induction and silence the

chromatin by heterochromatization. Heterochromatization is achieved by histone methylation and histone deacetylation at specific loci. One such protein is known as flowering locus C (FLC). FLC acts as a repressor. Cold treatment in fact induces few FLC antagonizing genes and FLC dissociates from the loci and get degraded or remain free. There are several other genes involved like VRN1, VRN2, VRN3 and VIN3. Even Frigida (FRI) proteins are involved. Frigida promotes FLC and FRI which antagonize FLC. Once the chromatin is free from FLC and its associated protein, they interact with floral integrators such as SOC, CO, FT and LFY, which in turn activate genes for floral parts. In certain cases GA can overcome vernalization.

ABC Model of flowering

In 1991 the ABC model was proposed to explain how homeotic genes control organ identity. The ABC model postulates that organ identity in each whorl is determined by a unique combination of the three organ identity gene activities (Figure 1):

- Activity of type A alone specifies sepals.
- Activities of both A and B are required for the formation of petals.
- Activities of B and C form stamens.
- Activity of C alone specifies carpels.

The model further proposes that activities A and C mutually repress each other; that is, both A and C-type genes have cadastal function in addition to their function in determining organ identity. The patterns of organ formation in the wild type and most of the mutant phenotypes are predicted and explained by this model. The challenge now is to understand how the expression pattern of these organ identity genes is controlled by cadastal genes; how organ identity genes, which encode transcription factors, alter the

pattern of other genes expressed in the developing organ; and finally how this altered pattern of gene expression results in the development of a specific floral organ.

Genetic aspects of flowering

Recent genetic studies have established that there are four genetically distinct developmental pathways that control flowering in the LDPA rhabdopsis (Blazquez, 2000). Figure 2 shows a simplified version of the four pathways: 1. The photoperiodic pathway involves phytochromes and cryptochromes. The interaction of these photoreceptors with a circadian clock initiates a pathway that eventually results in the expression of the gene CONSTANS (CO), which encodes a zinc-finger transcription factor that promotes flowering. CO acts through other genes to increase the expression of the floral meristem identity gene LEAFY (LFY). In the dual autonomous/vernalization pathway, flowering occurs either in response to internal signals—the production of a fixed number of leaves—or to low temperatures. In the autonomous pathway of Arabidopsis, all of the genes associated with the pathway are expressed in the meristem. The autonomous pathway acts by reducing the expression of the flowering repressor gene FLOWERING LOCUS C (FLC), an inhibitor of LFY (Michaels and Amasino, 2000). Vernalization also represses FLC, but perhaps by a different mechanism (an epigenetic switch). Because the FLC gene is a common target, the autonomous and vernalization pathways are grouped together. The carbohydrate, or sucrose, pathway reflects the metabolic state of the plant. Sucrose stimulates flowering in Arabidopsis by increasing LFY expression, although the genetic pathway is unknown.

The gibberellin pathway is required for early flowering and for flowering under noninductive short days. All four pathways

converge by increasing the expression of the key floral meristem identity gene AGAMOUSLIKE 20 (AGL20). Once turned on by AGL20, LFY activates the floral homeotic genes—APETALA1 (AP1), APETALA3 (AP3), PISTILLATA (PI), and AGAMOUS (AG)—that are required for floral organ development. APETALA2 (AP2) is expressed in both vegetative and floral meristems and is therefore not affected by LFY. Besides serving as a floral homeotic gene, AP1 functions as a meristem identity gene in Arabidopsis because it is involved in a positive feedback loop with LFY. Subsequently, once the transition to flowering has reached this stage, flowering is irreversible.

Physiology of flowering in Apple

Flower bud development starts during the previous season and flowering occurs in next spring in pome fruits. In apple initiation generally starts with the cessation of shoot growth (Imani and Abadi, 2011). The cycle of flower development often lasts from 9 to 10 months, but only a short interval of time is due to an active passing of this process, namely at the appearance and formation of the floral primordia in summer and at the final formation of flower parts in spring (Kolomietz, 1976). The period of relative dormancy permits the buds to pass a complete cycle of their development in two successive calendar years. Due to this the competition for nutrients between the developing flowers and vegetative parts is decreased, thus presenting a great advantage for the perennial fruit tree species, including apple in comparison with annual plants (Jackson and Sweet, 1972). The flower bud formation in the apple permits in the following succession: induction of flower bud formation, histological transformation and morphological differentiation (Buban and Faust, 1982). Flower bud induction gives an impulse to the sufficiently developed and

‘susceptible’ buds to transition from vegetative to generative phase (Dolega *et al.*, 1997). The fundamental reasons for induction are still not clear (Buban, 1996, Link, 1992). It could be supposed that this is a qualitative change, the final result of which can be programming of the strategically disposed parts from the meristem to forming flowers (17). The induction can also be viewed as a process during which previously repressed information is being transformed to form a new structure, namely the flower bud. Type of AFL (Apple Floricaula/Leafy) genes are supposed to be included in the induction (68). According to Luck will the induction is connected with changes in the hormonal balance, and according to Sachs with changes in the distribution of assimilates in the apical meristem. The flower bud induction, as well as the fruit set and the fall of fruits or of primordia of different organs of the plant, depend on the interaction in space and time of its own growth substances and those retaining growth (Link). When a signal is received by apex of the still vegetative bud for differentiating as a flower bud, a sequence of events takes place which encounters histological differentiation (Buban and Faust, 1982). The mitotic activity becomes total for the whole apex changing its histological structure.

The central meristem is more unfolded and is now under the sub dermatogen. By this rearranging, but without any morphological changes in the apex, the histological transformation is carried out, and from that moment on the initiation of the flowers is irreversible. The structure of the apex in vegetative stage (A) and in reproductive stage (B). The apple flower bud consists of a shortened axis, usually carrying 21 formations, inserted in the spiral sequence (Abbot, 1977). It includes bud scales, transitional leaves, true leaves and bracts (a leaf form, lamina and stipules of which are

totally depressed). The axis terminates in primordium of the 'king flower' and the primordia of the lateral flowers are formed in the axils of the three bracts and the three upper leaves. A primordium of a vegetative bud is located under the whorl of the flowers in the axils of one or two of leaves. Out of this bud, during the vegetation, a bourse shoot is formed which can, in its turn, form a new flower bud. The morphological differentiation occurs only if the structure of a vegetative bud is complete (Buban, 1996). Once the primordia of the appendages described above have already been initiated the differentiation of flower primordia in apple can start. The total appendages formed before the appearance of the first indication for the transition of the buds from vegetative into reproductive state represents a 'critical number of nodes' This number is generally cultivar dependent, and varies from 16 to 20 (Hirst and Ferree, 1995a,b, Huang, 1996, Luckwill and Silva, 1979). The total number of appendages formed by the appearance of the sepals of the apical flower in the cluster is also specific for the cultivars and can be influenced by the ecological conditions and the ways of growing. (McLaughlin and Greene, 1991). For the formation of bracts and the initiation of flowers in their bases, it is necessary for the plastochrone (the time between the forming of the primordia of two neighboring organs) to be shortened to 7 days (Fulford, 1966b). The widening and slight swelling of the bud apices, when they become dome-like in shape, is usually accepted as the first visible indication of the transition from vegetative to reproductive state is (Abbot, 1977, Guimond *et al.*, 1998 a, Hirst and Ferree, 1995b, Hoover *et al.*, 2004, Huang 1996, Kolomietz 1976, McCartney *et al.*, 2001, Zeller, 1954). For a greater precision in determining the moment of transition to a reproductive state in the apple, the onset of bract initiation could be taken into (Fulford 1966b, Koutinas *et al.*, 2006). Different stages

of flower bud differentiation includes meristem flat, meristem domed, bracelets developing on terminal floral meristem, sepals developing on terminal floral meristem and sepals differentiating on lateral floral meristem.(Hoover *et al.*, 2015). Kofler studied five apple bud developmental stages. (1) narrow and flat vegetative apical meristem; (2) broad and swollen vegetative meristem; (3) doming of the apex as the first morphological sign of floral initiation; (4) formation of the inflorescence primordia; (5) differentiation of the inflorescence. Stages 1 and 2 are regarded as non-initiated, whereas stages 3 to 5 are considered as initiated.

Flowering process in Almond

Almond flower buds are borne laterally in leaf axils on long shoots and short spurs. The flower buds enclose a single, terminal flower, and, typical of *Prunus L.* species, no leaves. One to several flower buds can form on a single spur. Flower bud differentiation in almond generally coincides with its hull split stage.

Different developmental stages of almond are categorised as (Lamp *et al.*):

Stage 0 Vegetative (pre-reproductive): Bud scales.

Stage 1 Transition to reproductive state: Increase in meristem size.

Stage 2 Flower initiation: Apex forms elongate, broad dome. Bracts present.

Stage 3 Sepal initiation: Sequential initiation of five sepal primordia.

Stage 4 Petal initiation: Sequential initiation of five petal primordia.

Stage 5 Stamen initiation: Sequential

initiation of multiple stamen primordia.

Stage 6 Transitional/precarpel initiation:
Stamen initiation complete, concavity at apex.

Stage 7 Carpel initiation: Carpel visible at the center of the apex.

Factors affecting flowering

Temperature

The reported effect of temperature on flower initiation are contradictory. Warm temperatures advance flower initiation and cool temperatures retard it but otherwise do not have any direct effect (Abbott, 1984). Indirectly, however, temperature influences the intensity of initiation by its effects on the rates of shoot and fruit growth, high temperature stimulating shoot growth and so influencing flowering negatively (Abbott, 1984, Tromp, 1984, Zhu *et al.*, 1997). The general effect of temperature seems to be a balance between positive (direct) and negative (indirect) influences.

Apple fruit buds developed under warm conditions throughout the growing season are, however, later to break in spring (Abbott, 1984). The processes of accumulation of chilling units, entry into dormancy and bud development are delayed by warm conditions in autumn and early winter. Bud development continues through the winter (Abbott, 1984) but the rate at which it does so is very dependent on cultivar. In many fruit-growing areas temperature effects on emergence from dormancy, i.e. the meeting of winter-chilling and thermal time requirements to achieve budbreak, are of dominant importance. In cool-temperate climates temperatures in the early spring, prior to budbreak and independent of frost damage effects, largely predetermine yield (Jackson and Hamer, 1980, Jackson *et al.*, 1983, Lakso, 1994).

Abbott *et al.*, (1974) reported that daily temperature fluctuations around a mean of 14.5°C favoured flower initiation as compared with constant 14.5°C. Tromp (1976) comparing two temperatures (24 and 17°C) showed that flowering was stimulated at the lower temperature when applied from full bloom, but it was reduced when temperature was raised from 17 to 24°C seven weeks before harvest. Later Tromp (1980) suggested that the first 4-5 weeks after full bloom are of especially great importance for flower formation. In contrast, Schmidt (1973) and Luckwill (1975) are of the opinion that the temperature during the summer also affects flower initiation.

Recently, Verheij (1996) in an extensive study on flower-bud formation in apple, found that different cultivars did not respond similarly to temperature with respect to flowering. Total number of flower clusters and percentage of flower clusters for spurs and one-year old shoots were much higher at 20°C than at 13°C applied throughout the season (Table 1). At 27°C flower production increased even further on spurs but not on the one-year-old shoots. A rise in temperature from 13 to 20°C (13 + 20) in the middle of the season favoured flowering considerably on both types of wood. Increasing the temperature from 20 to 27°C (20 + 27) was not effective on spurs but stimulated flowering somewhat on the one-year-old wood (Zhu *et al.*)

Results may be brought into line when we assume that an increase of temperature directly favours flower-bud formation, but at the same time inhibits flowering via stimulation of shoot growth. The ultimate result depends on the relative importance of these two effects, which will probably not be the same in all situations and for all cultivars. By this reasoning, in the present experiment, the direct effect naturally predominated.

Crop load

The two key factors determining crop load in apple (*Malus × domestica* Borkh.) are flower density and fruit set (Hanke *et al.*, 2007). Since fruit set can be adjusted to some extent by flower or fruitlet thinning, the critical factor is the number of flower buds per tree (Dennis *et al.*, 2003). Fruit growers aim for stable numbers of flower buds across years to reduce the risk of triggering the phenomenon of biennial bearing (Jonkers, 1979). This cropping irregularity is characterized by large yields of small-sized fruit in 'on' years and low yields of over-sized fruit in 'off' years (Williams and Edgerton, 1981), i.e. trees with 'on'-bearing status change to 'off'-bearing status in the subsequent year and vice versa. Apple cultivars differ in their degree of biennial bearing behaviour, e.g. 'Gala' has a regular bearing habit, whereas 'Fuji' shows a strong tendency to bear biennially (Hampson and Kemo, 2003). Besides apple, biennial or alternate bearing is also commonly found in other fruit trees such as pistachio, pecan, olive, citrus, avocado or mango (Monselise and Goldschmidt, 1982).

The physiological reason for entering an 'off' year is supposedly the competitive overlap of flower bud formation for the subsequent season and fruit development during the current season (Pratt, 1988, Dennis and Neilson, 1998). Perennial fruit trees such as apple start their reproductive development early in the first growing season of a 2-year-cycle with inducing flower buds at the first stage of the flower bud formation process (Buban and Faust, 1982). During this stage, termed flower induction, the vegetative meristem perceives a specific signal that either promotes flower bud development by triggering various biochemical processes or suppresses factors that cause the meristem to remain in a vegetative state (Dolega and Link, 2015). For example, as recently shown (Xing

et al., 2015), sucrose could act as a signal molecule for mediating flower induction in apple. Several studies reported that high crop load inhibits flower induction in apple, leading to poor return bloom in the following year (Monselise and Goldschmidt, 1982, Schmidt *et al.*, 2009, Samuoliene *et al.*, 2016, Wilkie *et al.*, 2008, Wunsche and Ferguson, 2005).

The exact mechanism of crop load-induced inhibition of flower induction still remains unclear, although there is good evidence that a high yield reduces next year's flower density, hence crop load, in a specific way: mobile signals formed by developing fruit or specifically seed within the fruit (e.g. plant hormones such as gibberellins) (Hoad, 1978, Marino and Green, 1981, McCartney, 1994) or lack of certain nutrients (e.g. carbohydrates) (Monselise Goldschmidt, 1982) inhibit the nearby bud meristem. Moreover, high fruit load and high levels of gibberellins are accompanied by an increased expression of the TFL gene (Samach and Smith, 2013, Haberman *et al.*, 2016) and reduced expression of FT in apical buds (Kittikorn *et al.*, 2011) during flower induction. The first initiated 'Gala' buds were found 99 dafb, irrespective of treatment, and bud initiation was observed until the last sampling date at 127 dafb (Fig.) (Kofler, 2015). However, at each sampling time 'off' trees exhibited a much greater percentage of bud initiation than 'on' trees, resulting in average initiation percentages, calculated starting from the first sampling point where initiated buds were found until the last sampling date, of 87% and 33% for 'off' and 'on' trees, respectively. Bud initiation in 'Fuji' started in 'off' trees at 77 dafb, 22 days earlier than in 'Gala', but at 120 dafb in 'on' trees, yielding a mean percentage of initiation of 83% for 'off' trees and 17% for 'on' trees (Fig.). Effect of crop load can also be explained by the following figures 1-12.

Table.1 Effect of temperature on the total number of flower clusters per tree and on the percentage of flower clusters (developing from the total number of vegetative and generative buds) irrespective of quality (1) and the percentage of flower clusters having more than three well-developed flowers (from the total number of clusters) (2) for spurs and one-year-old shoots

Temperature	No of clusters	Percentage of flower clusters			
		Spurs		1 year old shoots	
		1	2	1	2
13	93	27	97	38	92
13-20	190	55	81	85	78
20	128	51	82	68	78
20-27	200	53	74	80	64
27	168	66	78	74	58

Fig.1 ABC Model of flowering

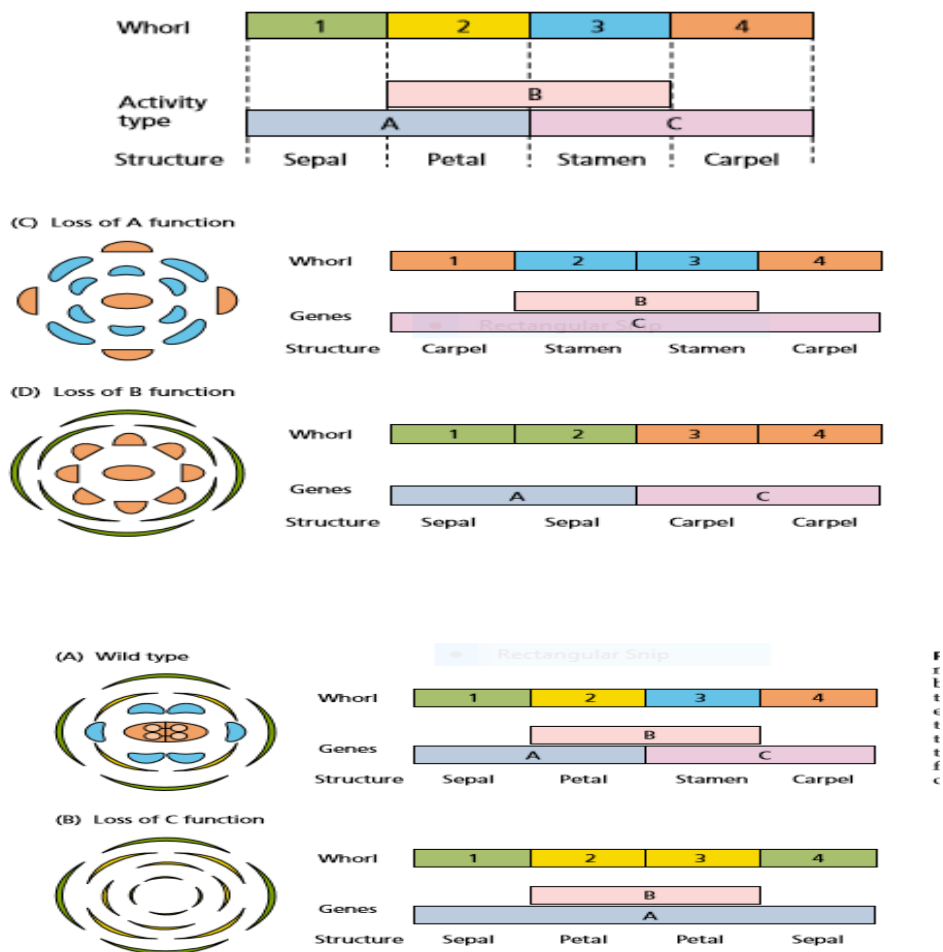


Fig.2 Genetic aspects of flowering

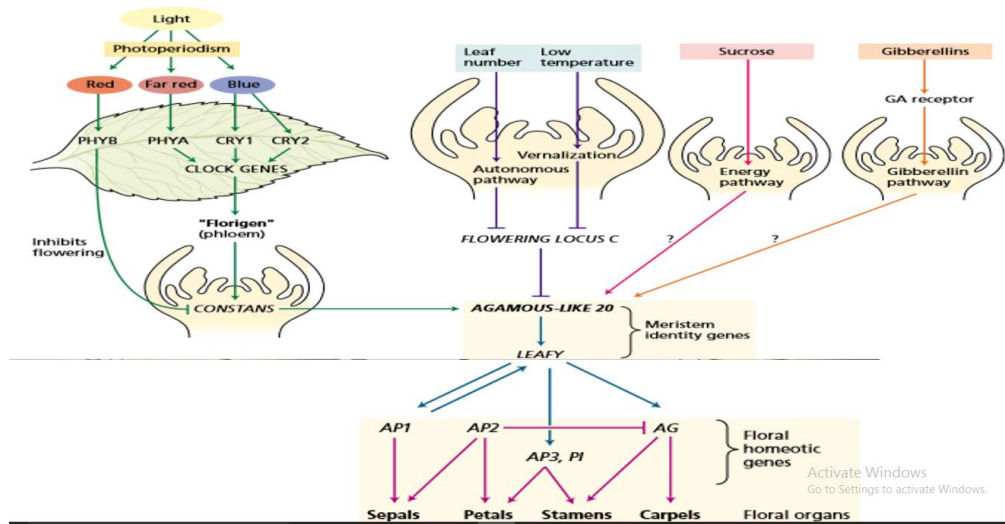
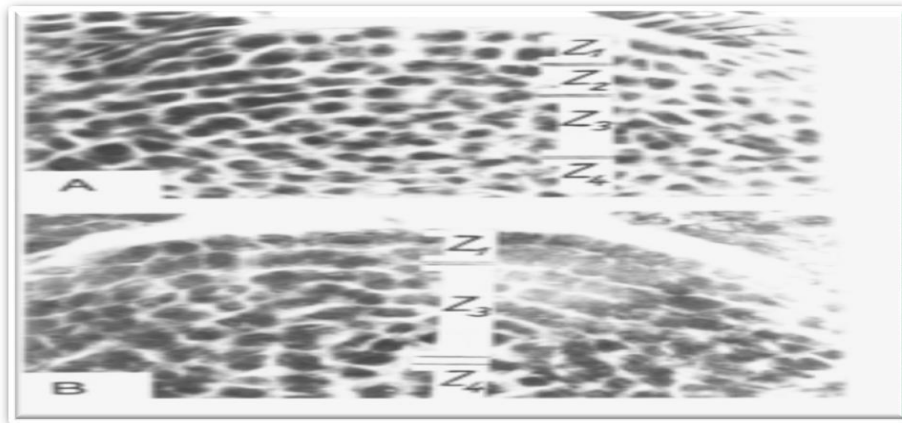


Fig.3



Z₁. dermatogen and sub- dermatogen. Z₂. accessory tunica layer. Z₃. central meristem. Z₃. pith meristem.

Fig.4

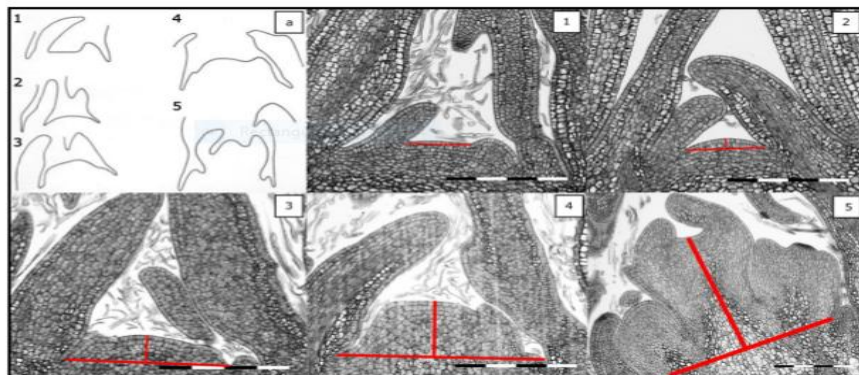


Fig.5

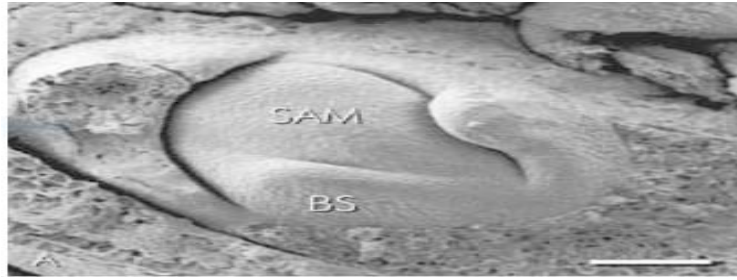


Fig.6

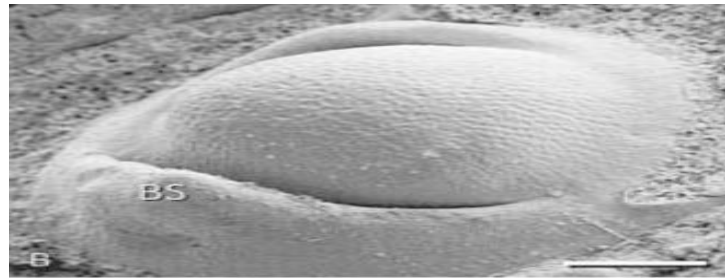


Fig.7

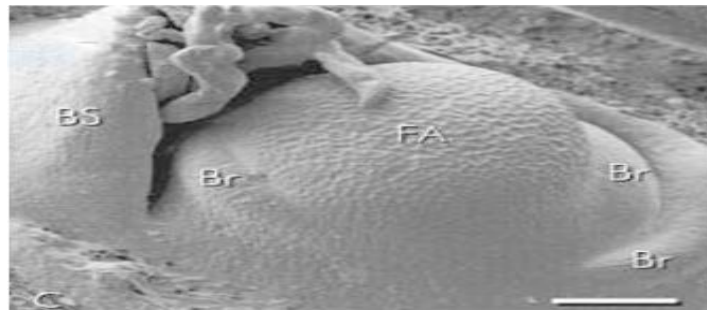


Fig.8

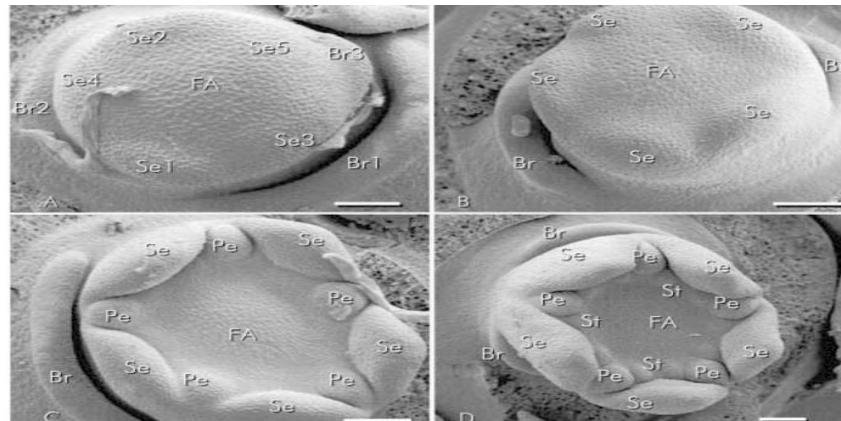


Fig.9

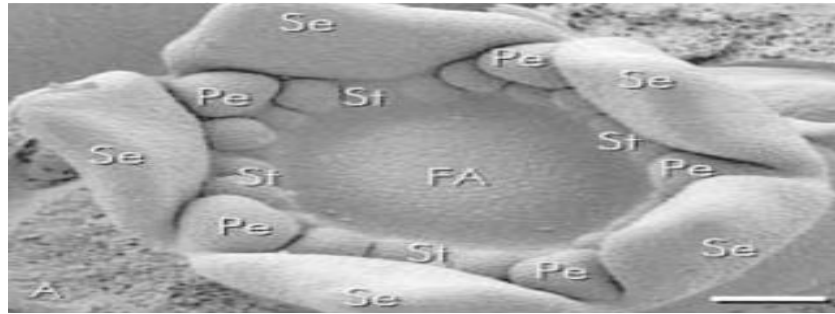


Fig.10

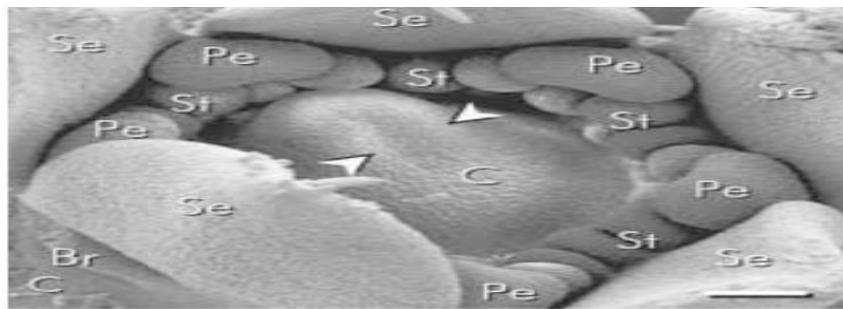


Fig.11

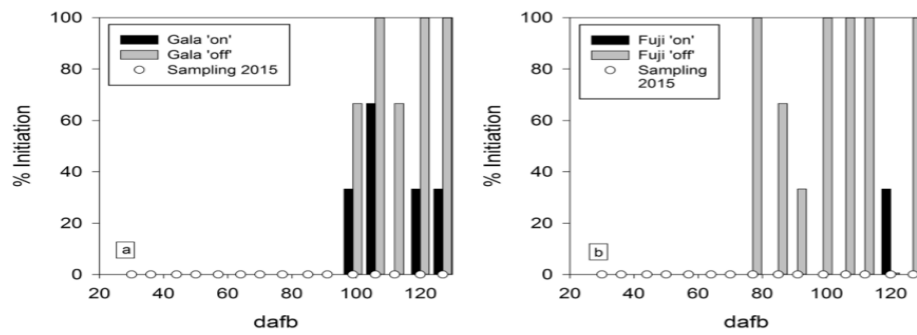
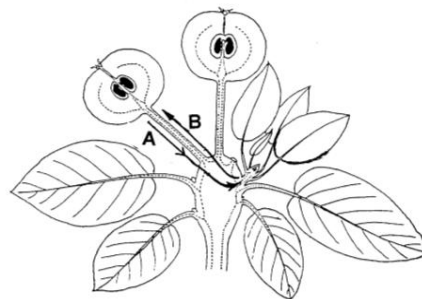


Fig.12



Inhibitor (GA) from seed moves to bourse shoot, where it prevents flowering. (B) Seed has priority for compound produced by leaves that promotes flowering (florigen?), thereby preventing flowering. (Dennis and Neilson 2005)

Cultivar/rootstock

The onset of the histological and morphological differentiation in apple may depend on the features of a cultivar. The cultivar can wield an influence also with respect to the further development of flower buds. Rootstocks on the other hand as components of the grafted fruit trees, may influence the time of initiation of flower buds. Some apple rootstocks exert this influence of the morphological differentiation and the share of spurs with initiated flower buds increased under the influence of dwarfing rootstocks. only on specific cultivars where an interaction between the two components of a tree takes place, leading to a change in the time of onset.

Fruit bearing branches

Differences in the time of initiation of flower buds on different types of fruit bearing branches have been commonly renowned. Bud differentiation usually starts at the earliest on the perennial spurs, somewhat later on the younger and more vigorous ones, and at the latest, on the shoots. Sometimes the onset of flower formation on branches with alike position can occur suddenly and almost simultaneously in all of them and in other cases within a much longer time.

Shoot growth

Differentiation of flower buds is often allied with the growth of the shoots. Termination of growth is considered as a requirement for flower initiation. The spurs stop their growth

2-4 weeks after the bloom whereas the shoots may continue their growth. According to Luckwill and Silva (1979), flower initiation in spur and axillary buds of 'Golden Delicious' apple, occurs about two weeks after growth cessation of long shoots, but it is one month later in the terminal buds of the shoots. Vegetative growth and flower bud formation are considered as antagonism, however, is not characteristic of all apple cultivars.

Influence of the fruit

The depressing influence of the fruit on flower bud formation is a common phenomenon in the fruit tree species with alternately bearing cultivars, such as apple. The reducing down influence on the flower bud formation according to Luckwill (1979) is hormonally based. Depression of flower bud formation by a part of fruits in the alternately bearing apple cultivars can be manifested by the prolonged plastochrone. In these cultivars it continues up to 18 days and is not favorable for flower initiation, where as in the regularly bearing cultivars the plastochrone is 7 days.

Cytochemical changes

The cytochemical changes happening in the buds and their neighboring organs and tissues, influence in some way their transition from vegetative to generative state. The increased content of nucleic acids and the decreased content of IAA favor the flower bud formation. The presence of fruit on spurs results in a decrease of the nucleic acid content and increase of the nucleohistone and this has a negative effect on the floral bud differentiation (Buban and Simon, 1978). Fruits also reduce the starch content in the fifth to sixth week after full bloom. According to Grochowthska (1973) the high starch content in the spurs cannot be regarded as a direct cause for flower bud initiation, but only

as an excellent and rapid indicator of the direction of metabolic processes resulting from the low amounts of auxin and gibberellins in the surrounding tissues. The Sachs, hypothesis (1977) for diverting assimilates, referring to the interrelation between the vegetative and the reproductive development deserves attention. According to this hypothesis the induction of flower bud formation provokes the activation of the central zone of the apical meristem of the bud, which is a necessary condition for initiating flowers and their early development in the presence of a big quantity of assimilates.

Hormones

Plant hormones (gibberellins, auxins, cytokinins, ethylene and growth inhibitors) performs numerous functions, which act simultaneously to regulate the behavior of fruit plants. Particular attention related to the flower bud formation in these plants has been paid to the gibberellins, which are determined as the fundamental factor for the lack of flower bud formation in the alternately bearing apple and pear cultivars (Luckwill, 1980). Depression of the flower bud formation with the purpose of overcoming the alternate bearing is also pragmatic in the application of the exogenous gibberellins up to the fourth week after flowering (Buban and Faust, 1982). The endogenous auxins and gibberellins act on flower bud formation, point out that auxins have an indirect, but favorable effect on the initiation of fruit buds at the beginning of the growing season. Auxins located in seeds, younger than four weeks, attract more nutrients to the spurs. This is important as the early, fast development of the leaf promordia and of young leaves early in the season, is a prerequisite for the flower bud initiation. The gibberellins, translocated from the seeds starting in the third to fourth week after full bloom, counteract the favourable auxin effect

and decrease flower bud formation. By means of enhancement of growth of shoots, they indirectly decrease flower bud formation. In the period, before the flower initiation, seeds of the alternately bearing apple cultivars diffuse considerably more gibberellins than seeds of regular bearing cultivar (Hoad, 1978).

Pruning

Influence of Dormant pruning on the growth and fruiting of the apple trees is well known fact while the studies on the summer pruning are very limited. Summer pruning, applied to young, vigorously growing apple trees, can be favourable for flower bud formation. It is desirable to be pruned in the first half of the summer. In some cases the summer pruning does not have any positive influence on the initiation of flower buds. Its effect depends on the characteristics of cultivars. Summer pruning can reduce the total number of flower buds per tree, but it can increase the number of flowers per inflorescence, so the total number of flowers per tree are not finally changed. For training tree crowns, the summer pruning is preferred over the dormant one, but it does not always result in an increase of yield. As far as dormant pruning is concerned, shortening of one year old shoots can be employed in the cultivars inclined to initiate flower buds on long shoots, with no negative effect on flower bud formation.

Use of fertilizers

Fertilization of fruit plants is a treatment that may considerably affect both the flower bud formation and fruit set. It must be done according to soil fertility, characteristics of the cultivars and rootstocks, climatic conditions, fruit load and desired fruit quality. Application of high doses of phosphorus at tree planting can increase the number of the initiated flower buds. Phosphorus is supposed

to influence indirectly flower bud formation by means of changing the level of the cytokinins synthesized in the roots. The nitrogen fertilization after conclusion of terminal growth of extension shoots may stimulate flower bud formation. The earlier application stimulates growth and this is undesirable for the potential flower bud formation. Summer fertilization with nitrogen as an addition to that applied in spring increases the vitality of ovules and stigmas in some apple cultivars. In the alternately bearing cultivars nitrogen fertilization in spring of the 'off' year must be limited, whereas the fertilization in autumn, as well as in spring of the following 'on' year should be abundant.

In conclusion the flower bud formation in fruit plants of the temperate climatic zone like apple is a very complicated biological phenomenon. However, some of the most characteristic moments of the bud transition from the vegetative into the reproductive state and their further development still not been sufficiently clarified. The existence of versatile relations is presumed, between the genetic control, the hormonal balance and the presence of sufficient amount of assimilates in the plant as a whole and more precisely in the forming flower buds.

The development of flower buds is related to the characteristics of the fruit tree species and cultivars, ecological conditions and agricultural practices. Quality of the reproductive organs depends on the factors and conditions for flower bud formation, which in turn influences the quantity and quality of fruit production. The initiation and development of flower buds in apple and other fruits can be successfully regulated by means of scientifically well-founded Agri-technical practices such as pruning, fertilization, irrigation and treatment with growth regulators.

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