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Physiology of Flowering- The Case of Mango

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Abstract
Mango (*Mangifera indiaca* L.) is the most important fruit of India belonging to family Anacardiaceae. Flowering, the first step of sexual reproduction is of paramount importance in agriculture, horticulture and plant breeding. The change from the vegetative state to the reproductive state is one of the most dramatic events in the ontogeny of a plant. Flowering leads to an exciting succession of events like anthesis, fruit set, fruit development, maturation and ripening. It provides for the propagation of the species and assists in crop improvement through genetic recombination. Mango occupied a pre-eminent place amongst the fruit crops grown in India because of its great utility. Mango exhibits a wide variation in flowering and fruiting habit due to varietal differences and diversity in agro-climatic conditions. It is highly cross pollinated crop contains male and hermaphrodite types of flower. The flowering mechanism of mango is very complex process and so many factors like physiological and environmental are affecting on it.

Keywords: Mango, flowering, growth regulators

Introduction
Mango is the fifth important fruit crop among the fruit crops cultivated in the world. India, where 40 per cent of the total fruits grown are only mango and it is regarded as national fruit of India. Mango exhibits wide variations in flowering and fruitting due to its strong dependency on environment. Flowering of mango is an important physiological event that sets the start of fruit production. Initiation is the first event that takes place for mangoes to flower. Flowering is decisive factor in the productivity of mango. The process associated with mango involves shoot initiation followed by floral differentiation of apical bud, and panicle emergence (Murti and Upreti, 2000) [18]. Variability of mango flowering depends upon cultivar, tree age, environmental condition and growth conditions in the dry or humid tropics (Singh, 1960) [22]. Mango is the premier fruit among the tropical fruits and has been in cultivated in the Indian subcontinent since several centuries. Mango is a terminal bearer and the phenomenon underlying switching from vegetative to reproductive mode is poorly understood. Mango is a tropical, evergreen fruit crop having strong tendency towards alternate or biennial bearing habit. Flowering in mango is very complex phenomenon making challenging for physiologists, breeders and growers. Several concepts were proposed by several researchers, but none of them holds good at least for one variety since the flowering in mango is being influenced by several factors. Flowering is one aspect of mango reproductive biology that has attracted interest from researchers worldwide. The present information will helps in better understanding of flowering physiology in mango and will cover the flowering behaviour of mango, factors affecting flowering, translocation of florigenic promoter (FP), a substance that is synthesized in leaves and is moved in phloem to buds where they are induce to flower and role of PGR in mango flowering.

The mango Flower
Mango trees are polygamous bearing both perfect and hermaphroditic flowers, having both pistil and staminate structures and purely male or stiminate flowers. Both types of flowers are born on same inflorescence *i.e*. and romonocious (Mukherjee and Litz, 2009) [16]. The mango inflorescence is basically terminal. The number of flowers in panicle may vary from 1000 to 6000 depending on the verity (Mukherjee 1953) [15]. Mango flowers are small (5-10mm)

in diameter, have a 10 part perianth consisting of four or five sepalsand petals that are ovate (Mukherjee and Litz, 2009) [16]. Both perfect and staminate flowers bear fleshy stamens (one and rarely two) and four sterile staminoids that are surrounded by gland (Galan-Sauco, 1999). Pistils- ovary abortion occurs early in staminate flower development and in perfect flowers, the ovary is superior. The ovule is anatropous and pendulous (Mukherjee and Litz, 2009) [16]. Individual flowers are borne collectively on panicles that consist of a central axis that further divides from primary, secondary and further pedicel architecture. Panicles develop from dormant apical buds or lateral buds during floral induction. Mango flowers usually open during the night and early morning hours and the flowering duration is usually of short *i.e.* 2 to 3 weeks. (Mukherjee, 1953) [15].

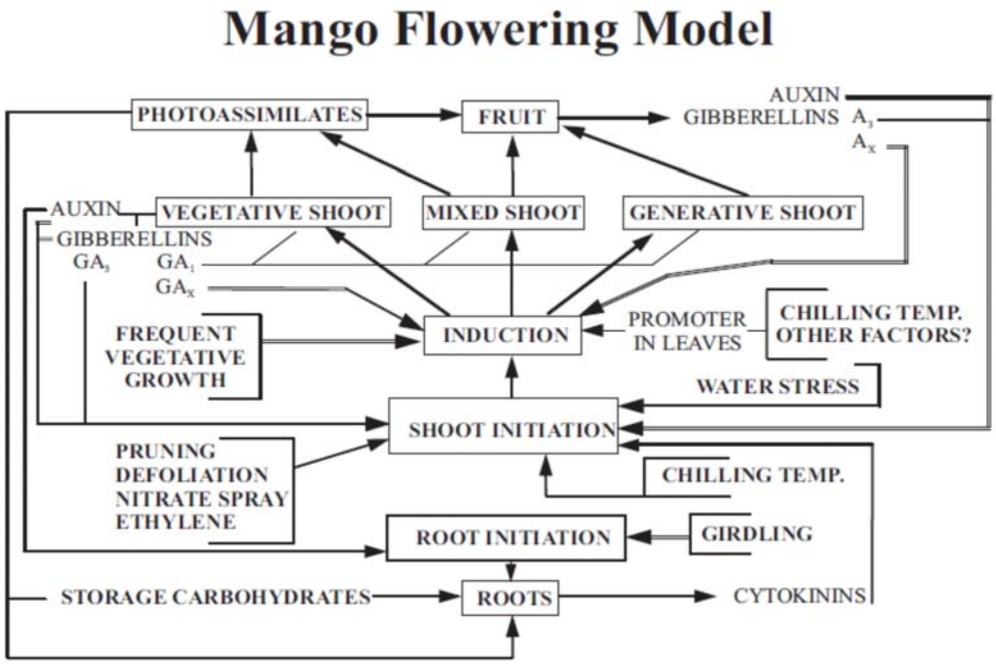

Fig 1: Conceptual flowering model of mango. The model summarizes the proposed roles for various phytohormones in initiation of shoot growth and in defining the vegetative or reproductive outcome of that growth (induction). Single lines in the scheme are promotive and double lines are inhibitory.

Factors governing flowering in mango

Flowering mechanism in mango is a complex and still poorly understood phenomenon. Besides genotypes, it clearly depends on environmental factors. Usually new vegetative flush appears and become mature, on which flowering occurs. After withdrawal of rainfall and dry spell, winter begins which triggers flowering in mango. Flowering usually occurs in three flushes in the season (Anon, 2013) [2]. Following factors are affecting on mango flowering.

Physiological factors

Vegetative growth & flushing episodes

Growth of mango is not continuous. It occurs as intermittent, short lasting flushes from apical buds and lateral buds. Generally, a healthy mango shoot completes four to five flushes per year depending upon cultivar and growing conditions. New shoots as primary growth arise as laterals from axillary buds around the fruited twigs of the previous year. Extension growth is extension of terminal portion of shoots already produced. Primary growth and extension growth depends on the variety and environment under which they are grown. The vegetative or reproductive fate of the resting buds is not pre-determined at the time of shoot initiation (Ramirez and Davenport, 2010) [20]. Mango trees produce basically three types of shoots viz. (i) vegetative shoots which bears only leaves, (ii) generative shoots which bears terminal panicles and (iii) mixed shoots produces both leaves and inflorescences within the same internodes. Vegetative shoots undergo distinct changes from early shoot development to maturation of leaves. Initially during elongation green stage (EGL) the shoots are light green in colour. They acquire reddish colour two weeks after initiation of bud break and little lignifications resulting in vertical hanging down of leaves from stems during Limp red leaf (LRL) stage. New leaves soon after return to light green and continue to strengthen by increased lignifications in the cell walls. One to two months after LRL stage turning to dark green colour reaching mature green leaf (MGL).

Florigenic promoter

Existence of florigenic promoter (FP) induces flowering in angiosperms. Florigenic promoter is continuously synthesized in mango leaves and its synthesis is governed by temperature. FP is translocated through phloem to apical buds and it was confirmed by girdling experiments. Branches which were girdled to isolate from the rest of tree and defoliated completely produced only vegetative shoots (Ramirez and Davenport, 2010) [20]. It is temperature regulated and vegetative promoter (VP) is age dependant. High ratio of FP/VP favours floral induction, low FP/VP favours vegetative growth and intermediate ratios favours mixed shoots. Florigenic promoter is up regulated on exposure to cool temperature (<18 C) in sub-tropical conditions. In tropics, regardless of temperature floral induction occurs in terminal stems that have attained sufficient time to rest of at least 4-5 months depending on cultivar. VP is gibberellin or closely associated with gibberellin synthesis pathway. To induce flowering in warm conditions the levels of VP must drop to sufficiently low levels with stem age (4months) to raise the FP/VP ratio.

Number of leaves

Singh (1971) [23] through ringing and defoliation experiments demonstrated that, presence of leaves was necessary for flower bud differentiation in mango. Flower inducing compounds will be supplied by leaves was some hormone similar to the hypothetical florigen. According to Davenport (2007), site of florigenic promoter's synthesis is leaves.

Environmental factors

Temperature

One of the main environmental factors influencing mango flowering is temperature. Cool temperatures of 15^0 C day/10^0 C, night induce flowering in subtropical condition. (Davenport and Nunez-Elisea 1997) [11]. Similarly flowering can also be affected by cool temperatures in high altitude tropics. Timing of initiation of reproductive shoots varies among cultivars. Very high and very low temperature during flowering is harmful to pollen and tree fails to flower. The main limiting factor of mango tree survival is severe frost. Thus, mango is best grown in areas that are frost free or that are subject to only occasional light frosts (Dag *et al*., 2000) [7].

Role of phytohormones and carbohydrates of flowering in mango

Flowering is decisive factor in the productivity of mango (*Mangifera indica* L). The process associated with mango involves shoot initiation followed by floral differentiation of apical bud, and panicle emergence (Murti and Upreti, 2000) [18]. All these developmental events occur in most of the mango cultivars sometimes during October-December under tropical as well as subtropical conditions. The induction of floral bud formation has strong links to prevailing environmental conditions and age of terminal resting shoots (Davenport, 2007) [9] as under tropical locations, the flower induction occurs in response to age of previous year shoot, while cool inductive conditions are vital to floral induction under sub-tropical conditions. It is documented that a low temperature around 15-18°C and 6-8 months old matured shoots have a strong possibility for floral growth initiation (Nunez-Elisea and Davenport, 1991; 1995; Murti and Upreti, 2000) [18]. Ramirez and Davenport (2010) [20] illustrated the basic mechanism underlying mango flowering, involving an interaction between putative temperature dependent florigenic promoter and an age regulated vegetative promoter, with a high ratio in favour of florigenic promoter under low temperature conditions contributing to floral development. It is found that the florigenic promoter that is graft transferable and short-lived has potential to move long distances during cool conditions and carbohydrates in the donor tissues are anticipated as driving force in the transport of florigenic promoter (Davenport *et al*., 2006) [12]. However, the exact nature of florigenic promoter and mechanism by which it elicit floral responses is still not elucidated. It is found that the florigenic promoter has strong link to phytohormonal factors, which act in association with carbohydrate production and supply during differentiation for expression of floral responses (Davenport, 2009; Murti and Upreti, 2000) [10, 18].

Phytohormones are considered intrinsic signal molecules produced within the plant, and occur in extremely low concentrations. These regulate various cellular physiological processes and optimize metabolic activity in targeted cells locally and in other locations of the plant upon transportation. Flowering has strong links to the phytohormonal synthesis and balance in the developing reproductive organs. In mango, correlative evidences have been provided for the regulation of floral process by phytohormones more specifically by gibberellins employing exogenous applications of growth regulators. Some evidences of phytohormonal involvement are also available from measurements of phytohormones in various organs during flowering time. Besides, carbohydrates reserves depicted as key energy producing chemicals also play important role floral induction process in many crop species. The increased capacity of leaf phloem loading system is contributory to floral induction. Based on the postulate suggested by Sachs and Hackett (1983) [21] that increased assimilate supply to the shoot apex contributed to floral initiation, the strategic role for carbohydrates in the flowering process was established. Thus, the adequate availability or supply of carbohydrate reserves is crucial to floral bud development and floral initiation. This is well supported from the fact that a high endogenous ratio of carbon to nitrogen ratio in plants is stimulatory to flowering whereas a low C: N ratio favours vegetative growth (Corbesier *et al.*, 2002) [6]. In mango, Singh (1960) [22] demonstrated that initiation of flowering mainly depends on maintenance of higher C/N ratio. This builtup in C:N ratio vital for floral growth points towards definite increases in carbohydrates. Evidences also point on role of gibberellins in the carbohydrate mobilization by stimulating their degradation to hexoses (Jacobsen and Chandler, 1987) [14]. Thus, a reduction in gibberellins important to induction of flowering could favour carbohydrate accumulation for eliciting of flowering. Davenport (2009) [10] suggested that the maturity of terminal shoots and accumulation of carbohydrates in the shoot apex are in some way linked to the synthesis of the floral stimulus.

Role of gibberellins

Gibberellins are considered derivatives of tetracyclic diterpenoid compounds and exhibit wide array of physiological activities. In many perennial fruit species including mango, gibberellins have been shown to suppress floral process (Davenport, 2009; Murti and Upreti, 2000) [10, 18]. The floral inhibitory response of gibberellins depends upon concentrations, growth stage, and climatic conditions of the location. In contrast to delaying inflorescence initiation in cool temperatures, GA did not delay vegetative growth during warm temperatures, thereby revealing that GA prevents initiation of reproductive shoots of mango rather than inhibiting floral induction. Further, the differential responses of gibberellins are attributed as the consequences of prevailing endogenous concentrations levels of gibberellins in differentiating buds during application, variations in uptake pattern, besides bud sensitivities, age of shoots and cultural practices. There are limited evidences to show the mechanisms involved in the inhibition of floral initiation by gibberellins. It is believed that increased gibberellins might enhance or maintain the synthesis and production of other hormones and/or modify assimilate partitioning to suit for inhibitions in flowering.

Concentration of GA increased with in buds with increase in stem age. Chen (1987) [5] found highest level of gibberellins in sap during leaf differentiation and lowered at rest, panicle emergence and full flowering. Also the endogenous level of gibberellins in mango was high in "off' year shoot-tips than in "on" year shoot-tips, suggesting that the erratic flowering or failure of flowering during the "off' year may be associated with a higher gibberellins levels in the shoot-tips. The role of gibberellins in mango flowering is further confirmed from the finding of Upreti *et al*. (2013) [24] and Abdel Rahim *et al*. (2011) [1] that paclobutrazol inhibited gibberellins in mango buds concomitant with profuse induction in flowering.

Role of auxins

Auxins influence flowering in many perennial plants and increasing trends in auxins in many perennials is vital to floral induction. However, their direct role in mango flowering is still not conclusive. It is believed that these act in association with other phytohormones like ethylene, cytokinin or gibberellins through manipulation in cell elongation process.

Role of cytokinins

Cytokinins are compounds with a structure resembling adenine which promotes cell division. These compounds are considered important regulator of shoot meristematic activity and their high production in apical meristem during active growth facilitates reproductive morphogenesis.

Role of ethylene

The fact that smudging and external applications of ethrel stimulates mango flowering suggests ethylene plays important role in floral induction. This was confirmed subsequently from the analysis of endogenous ethylene concentration during flowering (Chen, 1985; Nunez-Elisea, 1991) [4]. We also found higher ethylene concentration in Totapuri and Neelum (regular) at flowering stage compared to juvenile Langra (biennial) during flowering (Murti and Upreti, 1996) [17]. Various indirect evidences linked to ethylene production such as extrusion of latex in terminal buds at flower initiation and leaf epinasty near apex during panicle growth also confirm involvement of ethylene in mango flowering process. Besides, KNO_3 has been shown to stimulate flowering under tropical condition in number of mango cultivars. As KNO_3 is suggested to induce ethylene production and efficacy of KNO_3 is suppressed by ethylene biosynthesis inhibitors, the involvement of ethylene appear an important factor in mango flower process.

Role of abscisic acid

Abscisic acid is a sesquiterpene derivative, which typically regulate numerous developmental processes and has an inhibitory effect on cell elongation. It also regulates adaptive stress responses in plants. As stress conditions are required floral morphogenesis, its increased concentrations is expected to facilitate floral growth though stress adaptive mechanism involving osmotic adjustment and synthesis of stress responsive genes. It also has influence on flowering through is effects on sucrose metabolism. In mango, studies dealing with ABA role in floral inductions have not been made in great detail. Chacko (1968) [3] was first to report the presence of certain inhibitors similar to abscisic acid in mango shoots. His findings that the shoots of 'Dashehari' during 'On' year and 'Totapuri' trees had relatively higher levels of this inhibitors during flower bud initiation than the shoots of 'Dashehari' in 'off' trees indicated that the inhibitors are important in the initiation of flowering in mango. Further, the observation that defoliation of ringed shoots of ' Dashehari' and 'Janardhan Pasand' 'On' trees activates vegetative buds in such shoots, suggested that the inhibitor produced in the leaves is necessary for checking vegetative growth (Singh, 1971) [23]. Since the abscisic acid is antagonistic to both gibberellins and auxins, thereby affecting cell elongation and thereby providing conditions for floral bud differentiation. Upreti *et al*. (2013) [24] found profound accumulation of abscisic acid in paclobutrazol untreated and treated trees of Totapuri during pre-burst stages and concluded its possible significance in creating situation for floral growth in differentiating buds.

Role of carbohydrates

The requirement of high C: N ratio for floral initiation, induction in C: N ratio by paclobutrazol (Upreti *et al*., 2013) [24] and induction of flowering through girdling (Davenport, 2009) [10] depicts that increase in carbohydrate availability is important attribute to floral initiation in mango. The C: N ratio differed with growth of shoots in the varieties, which reveals its dependence upon environmental conditions and prevailing metabolic balance. The positive association of floral bud initiation with C: N ratio shows that the increase in carbohydrate availability and translocation is vital to the floral initiation in mango (Shivu Prasad, 2014). Thus, shoots with higher carbohydrate content are expected to favour flower initiation provided inductive conditions are prevailed. For this a critical level of carbohydrate is desired to express flowering favourable activity. As reproductive growth is a high energy requiring developmental event, the requirement of high carbohydrate demand at flowering is obvious. We presume an expected balance in certain carbohydrates for eliciting flowering responses by suitably influencing some associated enzymes. The increase in carbohydrates are concomitant with changes in phytohormones and we expect that declining gibberellins levels would favour built of simple carbohydrates, as one of principal effect of gibberellins is to mobilize carbohydrates by stimulating their degradation to simple sugars. Thus, an environment where gibberellins are high, no starch accumulation can take place. However, gibberellins concentration needs to fall below threshold levels to show carbohydrate accumulation tendency and floral initiation. Distinct differences in carbohydrate pattern is seen in growing shoots and with approach of flowering consistently higher production of total sugars and reducing sugars in apical buds of untreated as well as paclobutrazol treated trees was witnessed with peak concentration available at bud burst (Shivu Prasad *et al*., 2014). Paclobutrazol induced increase in soluble sugars at flowering has also been reported in mango by Abdel Rahim *et al*. (2011) [1]. The increased carbohydrates demand is due to the outcome of enhanced photosynthetic rate as result of increased photosynthetic efficiency required for encouraging reproductive development process. In addition, Davenport (2007) [9] believed occurrence of putative florigenic promoter in mango leaves that is loaded into the phloem and actively translocated by mass flow generated by high concentration of photo assimilates for the induction of floral differentiation. Furthermore, the directional movement of sugars from photosynthesizing leaves to tissues requires high energy and as the floral inductive process is high energy consuming metabolic process; the requirement of high soluble sugars for the energy supply for floral development is well justified. The mass flow of assimilated sugars from the leaves might help in the transport of a florigenic promoter to facilitate production of generative buds.

Conclusion

Flowering of mango is an important physiological event that sets the start of fruit production. Initiation is the first event that takes place for mangoes to flower. Flowering is decisive factor in the productivity of mango. Flower bud differentiation and floral initiation in mango denotes distinct changes in phytohormones and mobilization of carbohydrates from source to sink, which depend by climatic conditions, shoot age and size, besides genetic characters. Very high and very low temperature during flowering is harmful to pollen and tree fails to flower. Consistent decline in gibberellins with profound increase in cytokinins and abscisic acid in combination with sufficient built-up of carbohydrates in the buds approaching bud burst stage ensure floral inductions in mango. The accumulation of abscisic acid in buds at floral initiation is contributory in optimizing leaf water potential and sap flow besides optimizing carbohydrate availability and cytokinins in sustaining differentiation activity in growing buds. Not all gibberellins exhibits similar physiological activity to elicit floral response and nature and type of gibberellins are variety dependent. Distinct carbohydrate accumulation takes place as buds attain floral differentiation phase and it possible phytohormones like gibberellins and abscisic acid may have link in facilitating carbohydrate accumulation. The floral bud differentiation is expected to starts from 5 to 7 months before the actual flowering, for which 6-8 months old shoots with sufficient carbohydrate reserves are important. The information on timing of floral bud differentiation is vital under a particular set of climatic conditions for a variety, to enable growers to schedule the manuring, irrigation and other cultural operations to have better yield.

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