



E-ISSN: 2278-4136

P-ISSN: 2349-8234

JPP 2018; 7(6): 2375-2382

Received: 10-09-2018

Accepted: 12-10-2018

Md. Aayesha Jameel

Department of Fruit Science,
College of Horticulture, Dr.
YSRHU, Anantharajupeta,
Andhra Pradesh, India

SM Rajesh Naik

Department of Fruit Science,
College of Horticulture, Dr.
YSRHU, Anantharajupeta,
Andhra Pradesh, India

C Madhumathi

Department of Fruit Science,
College of Horticulture, Dr.
YSRHU, Anantharajupeta,
Andhra Pradesh, India

D Srinivasa Reddy

Department of Entomology,
CRS, Tirupathi, Dr. YSRHU,
Andhra Pradesh, India

KT Venkataramana

Department of Fruit Science,
College of Horticulture, Dr.
YSRHU, Anantharajupeta,
Andhra Pradesh, India

Correspondence**SM Rajesh Naik**

Department of Fruit Science,
College of Horticulture, Dr.
YSRHU, Anantharajupeta,
Andhra Pradesh, India

Physiology of flowering in mango

Md Aayesha Jameel, SM Rajesh Naik, C Madhumathi, D Srinivasa Reddy and KT Venkataramana

Abstract

Mango flowering is an important physiological event that sets the start of fruit production. Initiation is the first event that takes place for mangoes to flower. Coincident with shoot initiation, induction occurs based on the conditions present at the time of initiation. Numerous studies with mango trees support the existence of a florigenic promoter (FP) that is continuously synthesized in mango leaves and induces flowering. Translocation experiments suggest that the FP is carried from leaves to buds in phloem. Induction appears to be governed by the interaction of the FP and a vegetative promoter (VP). Mango exhibits wide variations in flowering and fruiting due to its strong dependency on environment. Flowering is a 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. Variability of mango flowering depends upon cultivar, tree age, environmental condition and growth conditions in the dry or humid tropics. Mango is the premier fruit among the tropical fruits and has been cultivated in the Indian subcontinent since several centuries. Flowering is one aspect of mango reproductive biology that has attracted interest from researchers worldwide. The present information will help in better understanding of flowering physiology in mango.

Keywords: Florigenic promoter, flowering, initiation, physiological, vegetative promoter

Introduction

Mango is the fifth most important fruit crop cultivated in the world. In India, about 40 % of the total fruits grown are only mango and it is regarded as "National Fruit of India". India is the largest producer of mango in the world and is extensively cultivated in an area of about 2.237 m ha with a total production of 18.779 m MT (Anonymous, 2015) [2]. Andhra Pradesh is the leading producer of mangoes accounting to 2822.08 '000 MT from an area of 315.42 '000ha (Anonymous, 2015-16) [2]. India is also a prominent exporter of fresh mangoes to the world. The country has exported about 36329.01 MT of fresh mangoes to the world during the year 2015-2016 (Source: NHB, 2015, APEDA 2015) [2].

Flowering in mango is a very complex phenomenon and is a challenging task for physiologists, breeders and growers. Flowering is a decisive factor in the productivity of mango. The processes associated with mango flowering involve shoot initiation followed by floral differentiation of apical bud and panicle emergence (Murti and Upreti, 2000). Consequently, mango flowering can be enhanced during its normal season or manipulated to occur at other times of the year in the tropics. Florigen promoter (FP), a substance that is synthesized in leaves and is moved through phloem to the buds where they are induced to flower. Apart from this low temperatures around 15-18°C and 6-8 months old matured shoots have a strong possibility for floral growth initiation (Nunez-Elisea and Davenport, 1997; Murti and Upreti, 2000) [15, 18, 44].

Control of flowering allows growers to harvest their crops at the most profitable times. Increasing the season of availability improves competitiveness in the international marketplace, and promotes the most efficient use of resources as costs of inputs continue to rise. Hence, the present topic aims towards physiology of flowering and its implications in mango.

Floral biology of mango

Mango trees are generally polygamous in nature bearing male and hermaphrodite flowers on the same inflorescence *i.e.* andromonoecious (Mukherjee and Litz, 2009) [38]. The mango inflorescence is basically terminal. The number of flowers in panicle may vary from 1000 to 6000 depending on the variety (Mukherjee 1953) [42]. Mango flowers are small (5-10mm) in diameter, have a 10 part perianth consisting of four or five sepals and petals that are ovate (Mukherjee and Litz, 2009) [38]. Pistils-ovary abortion occurs early in staminate flower development and in perfect flowers, the ovary is superior.

The ovule is anatropous and pendulous. Individual flowers are borne collectively on panicles that consist of a central axis that further divides from primary, secondary and tertiary branches. 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.

Floral anthesis generally occurs at night in polyembryonic cultivars and at night or early morning in monoembryonic types. Stigmas are receptive from 18 h prior to anthesis to at least 72 h after anthesis with optimum receptivity within 3 h from anthesis (Randhawa and Damodaran, 1961) [50].

Flowering may start as early as November or usually during December in the Rayalaseema region of Andhra Pradesh and in the south Konkan region on the West Coast of India. It is believed that flower bud differentiation depends upon the ‘on’ and ‘off’ year phases of the tree rather than on the initial cessation of growth of shoots (Kulkarni and Reddy, 1983) [33].

Growth pattern and flushing episodes in mango flowering

Growth of mango is not continuous but it occurs as intermittent, short lasting flushes of shoots from apical or lateral buds. The flushing refers to the emergence of new shoots on the terminals of old shoots. Generally a healthy mango shoot completes four to five flushing episodes per year depending upon cultivars and growing condition (Davenport and Nunez-Elisea, 1997 [15, 18, 44], while blooming occurs on a few of them during the following year. Terminal inflorescences or panicles are initiated in dormant apical buds on stems that developed vegetative from lateral buds following the previous flowering seasons (Litz, 1997) [36].

Stems are different from shoots, which are growing structures that evoke from buds of stems. Vegetative shoots bear only leaves, whereas generative shoots produce inflorescences and mixed shoots produce both leaves and inflorescences within the same nodes. Initiation of shoot growth in buds of resting stems is the first event that must occur in order to produce flowering (Davenport and Nunez-Elisea, 1997 [15, 18, 44], Davenport, 2000, 2008) [23]. The vegetative or reproductive fate of resting apical or lateral mango buds is not predetermined at the time of shoot initiation.

New shoots arise mostly as laterals from axillary buds around the stump of the twigs fruited previous year. Terminal growth

is always in the form of an extension of shoots already produced. Growth occurs in different flushes which vary from variety to variety and under different environmental conditions. Under north Indian conditions, March-April and May-June are the most important periods for the emergence of new shoots. However, stray shoots and sporadic extension growth may emerge any time between July and October. Under south Indian conditions, two active flushes occurring from February to June and October to November were reported. Three main growth flushes in February to March, March to April and October to November were reported in western India (Singh, 1958) [53].

Based on earlier works, it was proposed that early initiation and cessation of growth, followed by a definite dormant period, will help the shoots to attain proper physiological maturity essential for fruit bud Initiation that means floral behaviour of a shoot influences by its physiological position within the canopy. In biennial bearing varieties, ‘on’ and ‘off’ year phases, rather than age and cessation of growth of shoots govern the flower bud differentiation in the trees. The shoot, depending upon the cultivar may stop putting forth extension growth after May or continue until September or later and the potential of this shoot to form flower buds will depend on the floriferous condition of the tree.

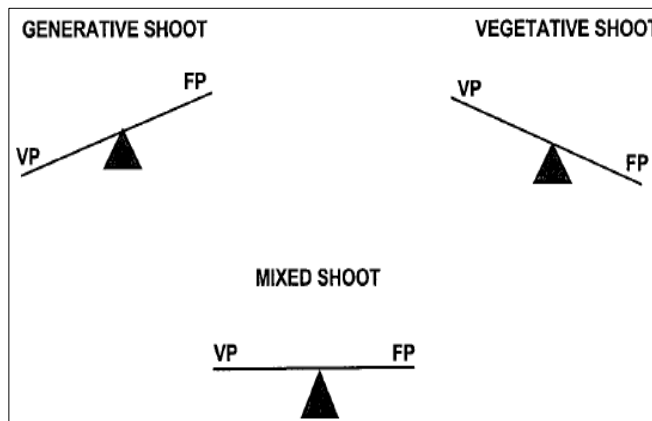


Fig 1: A low ratio of floral to vegetative promoter is conducive to formation of a vegetative shoot, whereas the inverse ratio is conducive to formation of a generative shoot. An even ratio of the two results in mixed shoots, forming both leaves and inflorescences in the same nodes.

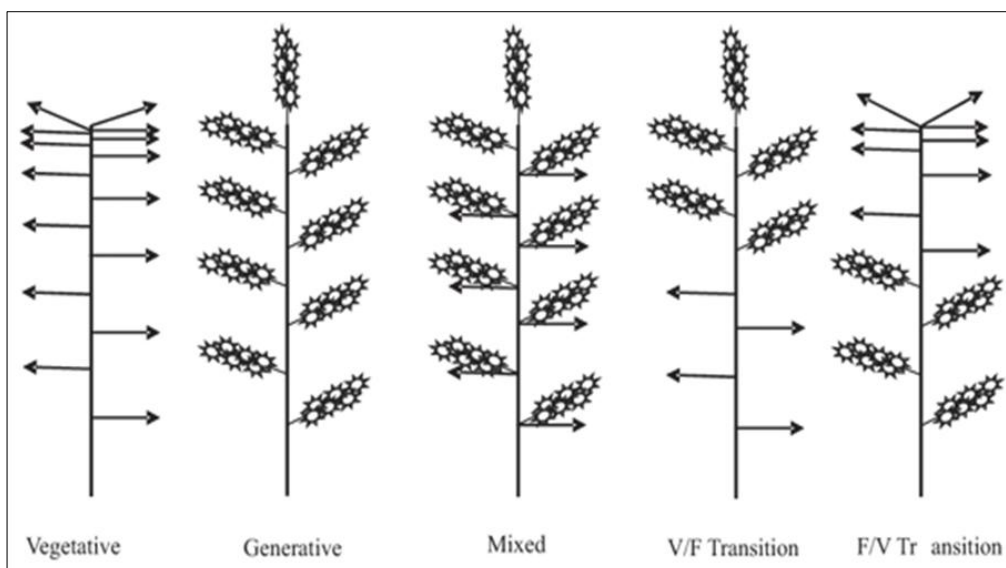


Fig 2: Stylized display of shoot types found in mango, Arrow (→) represents individual leaves, and floral diagram (⊛) represents lateral inflorescences

Shoot development

Flushes of vegetative extension growth of mango stems terminate with formation of determinate panicles. Several weeks to a few months after separation of the last flower or fruit from these panicles are required for the central axis of the panicle or rachis to dry and mechanically separate from the supporting stem, depending on the longevity of attached fruit. Five to ten lateral vegetative shoots typically develop from axillary buds located at the terminal intercalation positioned in a compact whorl surrounding the panicle scar of each stem (Reece *et al.*, 1949) [52]. These lateral shoots become the branch points of stems. These branching shoots form 10–15 leaves before the apical buds return to a resting state to establish them as individual stems. Initiation of these lateral vegetative shoots may occur 2–3 months after desiccation of panicles which fail to set fruit.

The apical resting bud of each newly established lateral stem (intercalary unit) is surrounded by a compact whorl of 10–12 leaves with short internodes (intercalation). Protective bud scales are green but may be brown at the tips due to desiccation. Resting buds possess a number of pre-formed nodes, each of which contains a leaf bract or leaf primordium and a lateral meristem (Chaikiattiyos *et al.*, 1994) [9]. The outermost, proximally located dried leaf bracts (bud scales) protect the more distal interior leaf bracts, leaf primordia and lateral meristems from mechanical damage and desiccation. Leaf bracts are vestigial non-developed leaves.

Shoots bearing only inflorescences (generative shoots) result from inductive development of lateral meristems and suppression of leaf primordial development. Mixed shoot induction results in combined development of leaf primordia and lateral meristems.

Vegetative shoots

Vegetative shoots bear only leaves. Vegetative shoots may arise either from axillary buds, if no apical bud exists due to flowering in the previous flush, or from the apical bud when present. Cells in the leaf primordia of initiating buds begin to form individual leaves in the proximal portion of the vegetative shoot. Soon thereafter, the apical meristem activates to form more nodes bearing leaf primordia and lateral meristems. These newly formed leaf primordia develop as the distal portion of the vegetative shoot if environmental conditions remain vegetatively inductive (Nunez-Elisea *et al.*, 1996).

Newly elongating vegetative shoots are green in most cultivars but may be bronze or red in others. Fully expanded leaves are a

shade of red, depending upon cultivar and cultural conditions and are thin and limp from lack of lignifications. The apical buds of vegetative shoots generally become quiescent before completion of the limp, red-leaf stage (Nunez-Elisea and Davenport, 1997) [15, 18, 44]. Fully expanded leaves become light green and stiff as they become lignified and suberized. Vegetative shoots are mature when leaves become dark green, which occurs when they are 2 or 3 months old.

Reproductive shoots

Two types of reproductive shoots typically occur in mango. Generative shoots display only flowers and have floral bracts or non-developed leaves at the base of each lateral inflorescence. The complexes of primary to quaternary branching lateral structures of the inflorescence each terminate with three cymose flowers. The terminal flower opens first, followed by two subtending lateral flowers. These complexes form the lateral inflorescence structures emerging from the central axis of the panicle. The central axis extension also terminates in a similar fashion (Mustard and Lynch, 1946 and Singh, 1958) [39, 53]. Generative shoot development in apical buds initially involves swelling of the lateral meristems and their bud scales. Each axillary meristem develops as an inflorescence on a primary peduncle.

Flowering mechanism models

Mango stems undergo varying periods of rest between episodes of growth, depending on tree age and environmental influences. Resting mango buds must, therefore, respond to two distinctly different signals for shoots to occur. The first signal initiates growth of the shoot and the second determines if it will be vegetative or reproductive. The signals that regulate initiation of shoot growth in resting buds differ from the inductive signals that regulate shoot type.

Several conceptual models have been proposed that attempt to explain the physiological basis of mango flowering. Each model should be viewed as a collection of integrated ideas, which require rigorous testing for validity within the context of the models. A useful model should explain how flowering and vegetative growth is regulated in all cultivars and races in both humid and dry climates in the tropics and subtropics. The flowering model is hormone-regulated.

Conceptual flowering model of mango

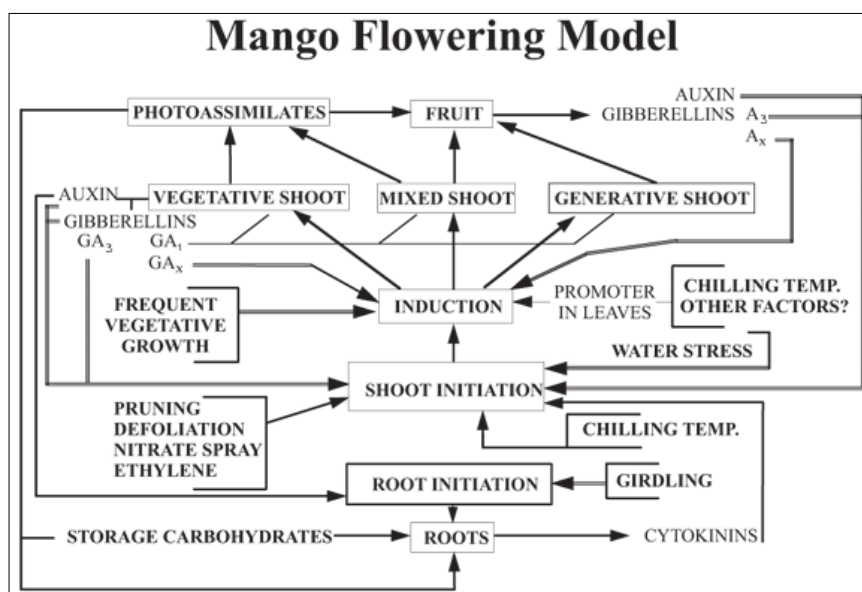


Fig 3: Conceptual flowering model of mango. The model summarizes the proposed roles for various phytohormones in initiation of shoot growth and in defining the vegetative or reproductive outcome of that growth (induction). Single lines in the scheme are promotive and double lines are inhibitory.

This is a model of flowering involving the various classes of phytohormones based on many lines of experimental evidence as well as on research of other tropical and subtropical fruit crops with similar phenological cycles (Davenport and Stern 2005) [24].

Two distinct events must occur for vegetative or reproductive growth to occur in resting apical or lateral buds of mango: (i) The bud must be initiated to grow (shoot initiation) and (ii) At the time of initiation, shoot development (i.e. vegetative, mixed, or generative) is determined (induction). Initiation and induction events are regulated by different signals and each may be manipulated by different stimuli.

First, the shoot itself must be initiated to grow, something must cause the bud to go from resting state to a growing state this is called initiation. Once it begins to grow, the second switch has to be turned one way or the other to determine what kind of growth will occur; vegetative (producing leaves) or generative (producing a panicle). Sometimes, a confused mixture of the two is produced, which we call a mixed shoot.

Shoot initiation occurs when optimal growth conditions (warm, humid weather) prevail, it will develop into a vegetative shoot. It involves cell division and elongation of cells in leaf primordia (vegetative shoots), lateral meristems (generative shoots) or both (mixed shoots) in the nodes of the resting buds, and is followed by cell divisions in the apical meristem to form more nodes. Shoot initiation is stimulated by pruning, defoliation and irrigation during dry conditions, or transition from the dry to rainy season in the tropics. Removal of apical buds by pruning stimulates initiation of axillary shoots. Defoliation of the apical whorl of five to ten leaves also stimulates shoot initiation in dormant apical buds (Davenport *et al.*, 2006) [14].

The photosynthates which the resulting leaves produce provide food for development of roots and other vital plant organs including fruit when available. They are either used immediately or stored in locations throughout the tree to be used at times when demand for carbon resources is greater than the current photosynthetic supply.

Vegetative shoots and fruit are also well known to be sources of two classes of plant hormones: Auxin and Gibberellins. These phytohormones may be involved in an internal cycle which regulates shoot initiation. For example, auxin is actively transported to roots from sites of production in shoots. Auxins are well known to stimulate root growth. This flush of root activity may either be a transient effect, or roots may grow somewhat continuously. Shoots are rich in auxins as they develop, auxins are transported specifically downward from the shoot to roots, and as leaves age we assume that their auxin production declines. Roots that develop from stimulation are known to be rich sources of cytokinins, which are major factors in stimulating shoot initiation. We envision a balance of shoot-produced auxin, diminishing as leaves age, and cytokinins in buds gradually increasing as they are transported upwards to buds and leaves through the xylem transpiration stream.

High auxin levels, compared to cytokinin levels, may inhibit shoot initiation, and high cytokinin levels, compared to auxin levels, may stimulate shoot initiation. During a rest period, auxin is possibly decreasing, cytokinins are increasing, and at some point, the bud's initiation of buds switch is triggered, stimulating it to grow. There is evidence that cytokinins have the effects that our model predicts. We have applied a synthetic cytokinin, such as 100ppm thidiazuron, to resting

buds. We obtained tremendous shoot initiation and proliferation in several experiments. If applied during an inductive period, *i.e.*, the wintertime, we got proliferation of inflorescences; if applied during the summertime under non-inductive conditions, we got either normal shooting or a proliferation of shooting.

Water stress inhibits shoot initiation by its direct impact on cell division and elongation possibly by interfering with translocation of cytokinins from roots. There is little evidence that water stress is directly involved in inductive processes. During water stress, roots continue to grow and produce cytokinins. Auxin synthesis and transport from leaves are reduced during water stress and may require several days for correction after rewatering. This rapid shift in the cytokinin/auxin ratio of buds may explain the shooting response that occurs soon after relief of water stress. GA3 may act with auxin to inhibit shoot initiation (Davenport *et al.*, 2006) [14].

Floral inductive condition assumes that a promoter is present in leaves. During an inductive (cool, winter nights), we girdled branches and de-blossomed the same branches and we defoliated some of those branches on day zero and did the same to other branches on days two, five and eight. All the growth resulting from the treatment at days zero and two was purely vegetative. There was an increase in generative shoots following the day-five treatment, with a further increase after day-eight treatment.

Hormonal regulation of shoot initiation and induction events results in reproductive shoot formation. During early shoot initiation, inductive signal shifted from floral (F) to Vegetative (V) or V to F, forming F/V or V/F transition shoots by altering temperature. Auxin from leaves and cytokinins from roots both are involved in initiation cycle under inductive temperatures. The minimum inductive period at 10/15°C (12h light/12h dark) required for complete floral induction and development was found to be 35 days for both cultivars namely *viz.*, Tommy Atkins and Keitt (Yeshitela *et al.*, 2004) [57, 58]. Management of off-season flowering in tropics accomplished successfully by synchronizing shoot initiation through tip pruning. Use of nitrate sprays coupled with management of the stem age to induce flowering such that it can be accomplished during any desired week of the year (Davenport, 2000) [23].

Florigenic promoter

Existence of florigenic promoter (FP) induces flowering in angiosperms. It is translocated through phloem to apical buds and it was confirmed by girdling experiments. Complete defoliation of girdled branches during inductive conditions results in vegetative shoots instead of generative shoots (Davenport *et al.*, 2000) [23]. 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. 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. Putative florigenic promoter is transported from adjacent branches to induce lateral flowering shoots on non-girdled, defoliated branches.

Tri-factor Hypothesis of Flowering Model

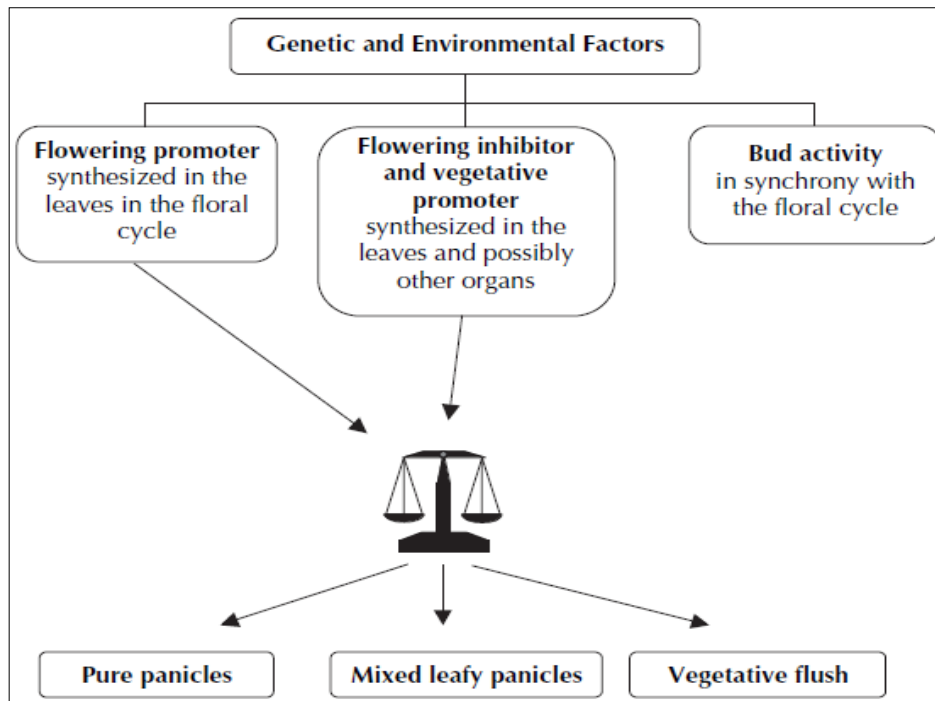


Fig 4: Kulkarni's Tri-factor Hypothesis of Flowering in mango, a hormone-regulated flowering model (Source: Kulkarni, 2004) ^[31].

The basis of a flowering model proposed by Kulkarni (1991) ^[30] the Tri-factor Hypothesis of Flowering in mango (Kulkarni, 2004) ^[31]. This theory proposes an interactive role for a putative, cyclically produced floral stimulus in leaves, a floral inhibitor in leaves and fruits, and bud activity during the floral cycle. During dormancy following a vegetative cycle, genetic and environmental factors determine the level of synthesis of the putative floral stimulus. Flowering occurs only if certain correlative factors are present, for example if the receptor bud becomes active. If fruits are or have been recently present on the stem, vegetative growth will result. Presence of the putative floral inhibitor in leaves interferes with expression of the floral stimulus resulting in vegetative growth. The level of the floral stimulus determines the response: high levels give rise to normal panicles, intermediate levels give rise to mixed panicles and low levels result in vegetative growth.

Environmental Influence on mango flowering

The effects of temperature and water relations on determining vegetative and reproductive growth of mango have been addressed (Davenport, 2000; Kulkarni, 2004) ^[23, 31]. This section focuses on the impacts of temperature, plant water relations, mineral nutrition and photoperiod on shoot initiation and induction.

Temperature

One of the main environmental factors influencing mango flowering is temperature. Cool temperatures of 15°C day/10°C night induce flowering in subtropical condition. (Davenport and Nunez-Elisea 1997) ^[15, 18, 44]. 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) ^[12].

Pollen viability

Flowers were stored at 5 °C and pollen viability was tested by the fluorochromatic reaction (FCR) test within 36 hours after collection (Peterson and Taber, 1987). After staining for a minimum of 5 min the sample (30-120 grains depending on the number of pollen from one anther) was examined under a fluorescence microscope (violet filter set, 405 and 435nm). Bright green- yellow fluorescence was taken to indicate viable pollen.

Hormonal influence on flowering

Phytohormones are directly involved as the FP. Phytohormones are intrinsic signal molecules produced within the plant, and occur in extremely low concentrations. Phytohormones appear to be responsible for shoot initiation in conditions that are floral inductive.

Possible interaction of phytohormones regulating shoot initiation

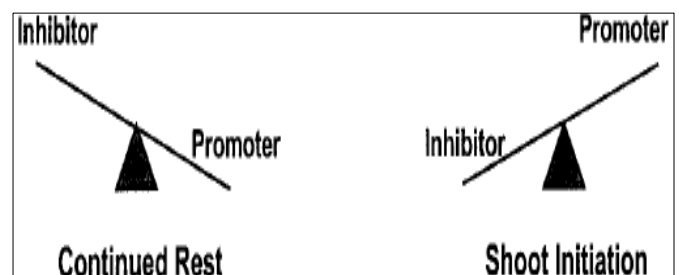


Fig 5: Possible interaction of phytohormones regulating shoot initiation (Davenport, 2000) ^[23]

Cytokinins from roots are proposed to serve as a promoter and auxin from leaves and fruit as an inhibitor of shoot initiation. Conditions conducive to a low ratio of promoter to inhibitor would result in continued rest of stem buds whereas a ratio above a threshold level would be conducive to initiation of new shoots regardless of shoot type (Davenport, 2000) ^[23].

Auxin

Chacko (1968) [7] found a high level of auxin-like substance in the shoots of 'Dashehari', which were expected to flower. The shoots from 'Dashehari' 'on' year and 'Totapuri Red Small' trees-initiated flower buds & had a higher level of growth promoting substances during the period of flower-bud initiation. Shoots of 'Dashehari' 'off' year trees which remained vegetative.

Gibberellins

Gibberellins are considered derivatives of tetracyclic diterpenoid compounds. In perennial fruit species including mango, gibberellins will suppress floral process (Davenport, 2009; Murti and Upreti, 1996) [13, 37]. GA₃ did not inhibit

floral induction, so long as cool, inductive temperatures were present during axillary shoot initiation. Chen (1987) [10] reported the highest levels of gibberellins in xylem sap during leaf differentiation and lower concentrations during rest, panicle emergence and full flowering.

Davenport *et al.* (2001) concluded that elevated GA₃ levels in buds may enhance or maintain the synthesis or activity of endogenous auxin to maintain low cytokinin/auxin ratios and enhance inhibition of shoot initiation. The activity of GA like substances – greater in "off" year and postulated that high levels of gibberellin inhibit flowering (Pal and Ram, 1978) [46].

Graph

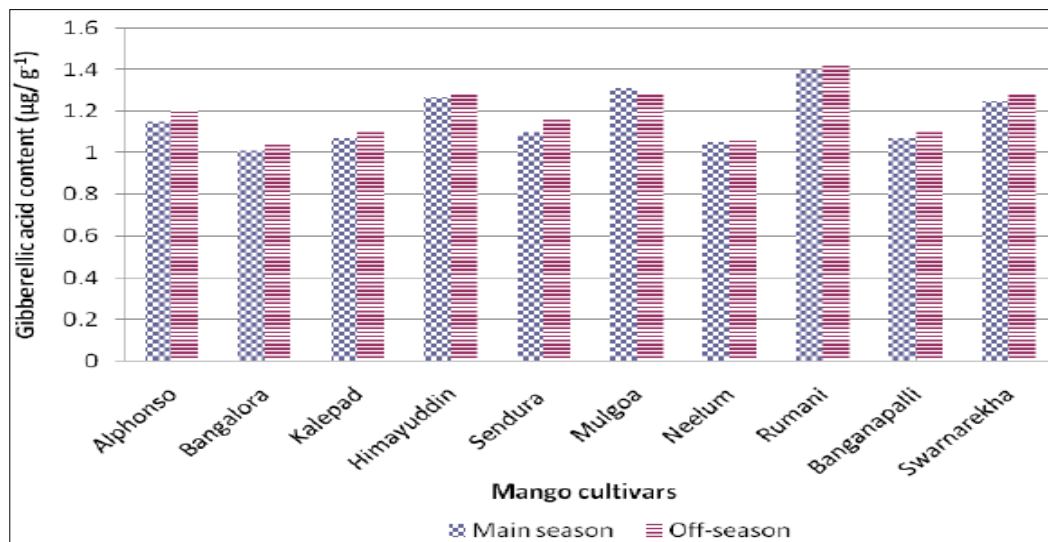


Fig 6: Pal S, Ram S. Endogenous gibberellins of mango shoot-tips and their significance in flowering.

Result

Gibberellic acid content were registered by Neelum during main season followed in Kale pad during main season (Pal and Ram, 1978) [46].

Cytokinins

Cytokinins structure resembling adenine which promotes cell division. Relationships between mango flowering and the endogenous levels of cytokinins in leaves, stem tips and xylem sap (Chen, 1987) [10] and the effect of cytokinin applications on bud break and shoot development. Chen (1985) [11] described precocious flowering of mango shoots in response to early October application of 6-benzylaminopurine (BA). Flowering was observed 1 month following application and 3 months later on non-treated trees. Cytokinin levels in mango stem buds increased during exposure to cool, floral inductive temperatures (Bangarath *et al.*, 2004) [3]. Cytokinin will occur at time of flower bud differentiation were higher in the 'on' year than in the 'off' year. A well-documented role for cytokinins in higher plants, especially evident *in vitro*, is bud organogenesis (Skoog and Miller, 1957) [55]. The primary cytokinins in higher plants are trans zeatin, Dihydrozeatin, isopentenyl adenine and their ribosides.

Ethylene

Smudging has been utilized to stimulate mango flowering in the Philippines. Only branches that attain sufficient age respond to smudging by forming reproductive shoots (Acala and San Pedro, 1935; Bueno and Valmayor, 1974) [1, 4], investigating smoke-induced flowering of pineapple,

proposed that ethylene, generated by burning material, may stimulate flowering. Dutcher (1972) [25] confirmed that smoke from smudge fires contained ethylene. Smudging and the use of ethephon in 1968 by F. Manuel (Barba, 1974) [5] and others (Bondad, 1972) to promote mango flowering suggested that endogenous ethylene is integral for floral induction.

Ethephon effectively promotes flowering of mangoes under specific conditions in the low-latitude tropics (Davenport and Nunez-Elisea, 1997) [15, 18, 44]. High ethylene content was observed in Totapuri and Neelum (regular) at flowering stage compared to juvenile Langra (biennial) during flowering (Murti and Upreti, 1996) [37].

Ethylene sprays

- Ethephon at the rate of 125-200ppm induced the flowering of 'Carabao' mango in the Philippines within six weeks after treatment (Dutcher, 1972) [25].
- In India (Ethephon) increases flowering in Langra and Dashehari ('off' years).
- It induces earlier production in juvenile plants (Chacko *et al.*, 1974) [8].

Abscise acid

Abscise 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 for 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 its effects on sucrose metabolism.

Chacko (1968) [7] was first to report the presence of certain inhibitors similar to abscisic acid in mango shoots. His findings that the shoots of 'Dashehari' 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.

Plant growth retardants

Plant growth retardants have been evaluated to stimulate early or more intense flowering, especially in the 'off' year of alternate-bearing cultivars (Davenport and Núñez-Elisea, 1997) [15, 18, 44]. They are in three main classes:

- i. The gibberellin transport inhibitor, daminozide (N-dimethylamino-succinamic acid), known as alar or B-Nine.
- ii. The onium type, chlormequat chloride (2-chloroethyl trimethylammonium chloride), known as cycocel.
- iii. The steroid-synthesis-inhibiting triazoles, for example PBZ (PP-333), known as Cultar.

Daminozide and Cycocel

The efficacy of daminozide and cycocel for increasing flowering in the 'off' season of alternate-bearing cultivars (Kurian and Iyer, 1994) [32]. Enhanced, inconsistent flowering occurs in response to these compounds, especially cycocel.

Triazoles

Paclobutrazol (PBZ), a synthetic plant growth regulator, was applied to mangoes to control vegetative growth and induce flowering. PBZ applied as a soil drench (1–20 g active ingredient (ai)/tree) reduces internode lengths and causes earlier and enhanced flowering in mango trees (Hasdiseve and Tongumpai et al, 1986) [29]. PBZ also reduces alternate bearing of some cultivars (Rao et al., 1997) [51]. Application of PBZ reduces the number of panicles, despite increased fruit set (Goguey, 1990) [27].

Paclobutrazol (PBZ)

Paclobutrazol is a gibberellins bio-synthesis inhibitor. Burondkar and Gunjate (1993) [6] reported that effect of PBZ on Alphonso at (RFRS) Vengurla - suppress the emergence of vegetative flush and length of vegetative shoot in 2 successive cropping years. Paclobutrazol application in mid of July, reduces the number of shoots per terminal in Alphonso, Kesar and Rajapuri. Reduction in vegetative growth in trees treated with Paclobutrazol (Hoda et al., 2001) [28].

Disadvantages of Paclobutrazol

Paclobutrazol is applied to soil in excess, under certain conditions, subsequent growth and normal development can be severely disrupted.

References

1. Acala PE, San Pedro A. Bud differentiation in smudged mango trees. *Philippine Agriculture*. 1935; 24:27-48.
2. Anonymous. *Horticultural Statistics at a glance*, GOI and APEDA, 2015, 463.
3. Bangerth F, Naphrom D, Sruamsiri P, Hegele M, Boonplod N, Manochai P. Hormonal changes in various tissues of mango trees during flower induction following cold temperature. *Acta Horticulturae*. 2004; 645:453-457.
4. Bueno PB, Valmayor RV, Potassium nitrate: key to mango flowering. *Agriculture Los Banos*, 1974, 13, 4-16.
5. Barba RC. Induction of flowering of the mango by chemical spray. *Proceedings of the Crop Science Society of the Philippines*. 1974; 5:154-160.
6. Burondkar MM, Gunjate RT. Control of vegetative growth and induction of regular and early cropping in Alphonso mango with paclobutrazol. *Acta Horticulturae*. 1993; 341:206-215.
7. Chacko EK. Studies on the physiology of flowering and fruit growth in mango. (*Mangifera indica* L.). Ph.D. thesis submitted to P. G. School of IARI, 1968.
8. Chacko EK, Kohli RR, Randhawa GS. Investigations on the use of 2-chloroethylphosphonic acid (Ethephon CEPA) for the control of biennial bearing in mango. *Scientia Horticulturae*. 1974; 2:389-398.
9. Chaikiattiyos S, Menzel CM, Rasmussen TS. Floral induction in tropical fruit trees: effects of temperature and water-supply. *Journal of Horticultural Science*. 1994; 69:397-415.
10. Chen WS. Endogenous growth substances in relation to shoot growth and flower bud development of mango. *J Amer. Soc. Hort. Sci*. 1987; 112:360-363.
11. Chen WS. Flower induction in mango (*Mangifera indica* L.) with plant growth substances. *Proc. Natl. Sci. Council Part B, Life Sci. Taipei, Rep. China*. 1985; 9:9-12.
12. Dag, A, Eisenstein D, Gazit S. Effect of temperature regimes on pollen and effective pollination of 'Kent' mango in Israel. *Scientia Horticulturae*. 2000; 86(1):1-11.
13. Davenport TL. Reproductive physiology. In: (Ed. R.E. Litz). *The Mango: Botany Production and Uses*, 2nd edition. CAB International, Wallingford, UK, 2009, 97-169.
14. Davenport TL, Zhang T, Ying Z. Isolation of potentially regulating mango flowering. *Proceedings of the 33rd annual meeting of the Plant Growth Regulation Society of America*, Quebec City, Canada, July 9–13, Plant Growth Regulation Society of America, Alexandria, 2006, 109-110.
15. Davenport TL, Nunez-Elisea. Reproductive physiology. *The Mango: botany, production and uses*. Wallingford: CAB International, 1997, 69-146.
16. Davenport TL, Nunez-Elisea R. Ethylene and other endogenous factors possibly involved in mango flowering. *Acta Horticulturae*. 1990; 275:441-448.
17. Davenport TL. Beneficial effects of water stress. In: Davenport, T. L. and Harrington, H.M. (eds.) *Proceedings of the Plant Stress In the Tropical Environment*. VSDA/CSRS/CBAG, Gaomesville, Florida, 1992, 16-20.
18. Davenport TL, Nunez-Elisea R. Reproductive physiology. 1997, 69-146.
19. Davenport TL. Citrus flowering. *Hort. Rev.* 1990; 12:349-408.
20. Davenport TL. Management of flowering in three tropical and subtropical fruit tree species. *Hort. Science*. 2003; 38:1331-1335.
21. Davenport TL. Avocado flowering. *Hort. Rev.* 1986; 8:257-289.
22. Davenport TL, Morgan PW, Jordan WR. Reduction of auxin transport capacity with age and internal water deficits in cotton petioles. *Plant Physiol*. 1980; 65:1023-1025.
23. Davenport TL, Pearce DW, Rood SB. Correlation of endogenous gibberellic acid with initiation of mango shoot growth. *J Plant Growth Reg.* (in press), 2000.

24. Davenport TL, Stern RA. Flowering. In: Menzel, C.M. and Waite, G.K. (Eds) Litchi and Longan: Botany, Cultivation and Uses. CAB International, Wallingford, UK, 2005, 87-113.
25. Dutcher RD. Induction of early flowering in 'Carabao' mango in the Philippines by smudging and ethephon application. Hort. Science. 1972; 7:343.
26. Dutta P. Effect of foliar application on panicle growth, fruit retention and physico-chemical characters of mango cv. Himsagar. Indian Journal Horticulture. 2004; 61(3):265-266.
27. Goguet T. Study of the effects of three flower-inducing substances on Kent and Haden mango (*Mangifera indica* L.). Am. J Bot. 1990; 36:734-740.
28. Hoda MN, Singh S, Singh J. Effect of cultar on flowering, fruiting and fruiting mango. Scientia Horticulturae. 2001; 2:389-398.
29. Hasdiseve C, Tongumpai P. Effects of paclobutrazol on vegetative growth, flowering, and fruiting of mango 'Nam Doc Mai Twai #4'. In: Proceedings of the National Conference. Kasetsart University 24, Bangkok, Thailand, 1986, 295-302.
30. Kulkarni VJ. Physiology of flowering in mango studied by grafting. Acta Horticulture. 1991; 291:95-104.
31. Kulkarni VJ. The tri-factor hypothesis of flowering in mango. Acta Horticulture. 2004; 645:61-70.
32. Kurian RM, Iyer CPA, Murti GSR. Total phenols of stem apical bud in relation to tree vigour in mango. Gartenbauwissenschaft. 1994; 59(6):268-270.
33. Kulkarni, Reddy. Studies on regulation of growth, flowering and fruit drop in mango (*Mangifera indica* L.), cv. Alphonso. This abstract, Haryana Agriculture University, 1983, 334-345
34. Kumar M, Ponnuswami V, Jeya Kumar P, Saraswathy S. Influence of season affecting flowering and physiological parameters in mango. Academic Journals. 2014; 9(1):1-6.
35. Kraus EJ, Kraybill HR. Vegetation and Reproduction with Reference to the Tomato. Bulletin of the Oregon Agricultural Experiment Station Number 149. Oregon State University, Corvallis, Oregon, 1918.
36. Litz RE. The mango, Botany, Production and Uses. First ed., CAB International. Univ. Press, Cambridge, N.Y. 1997, 587.
37. Murti GSR, Upreti KK. Changes in the levels of endogenous hormones in relation to shoot vigour in mango (*Mangifera indica* L.). Plant Physiol. & Biochem 1996; 25(2):167-171
38. Mukherjee SK, Litz RE. The mango: Botany production and uses. 2nd edition. CAB international, Wallingford, UK, 2009.
39. Mustard MJ, Lynch SJ. Flower-bud formation and development in (*Mangifera indica*) of regular and early cropping in 'Alphonso' mango with paclobutrazol. Acta Horticulture. 1946; 341:206-215.
40. Mukherjee SK. Origin of Mango. Indian J Genet. Pl. Breed. 1951; 11:49-56.
41. Mukherjee SK. Cytology and Breeding of Mango. Punjab Hort. J 1967; 3:107-15.
42. Mukherjee SK. The mango- its botany, cultivation, uses and future improvement, especially observed in India. Economic botany, 1953; 7(2):130-162.
43. Nunez-Elisea R, Davenport TL, Caldeira ML. Control of bud morphogenesis in mango (*Mangifera indica* L.) by girdling, defoliation and temperature modification. J Hort. Sci. 1996; 71:25-40
44. Nunez-Elisea R, Davenport TL. Flowering of mango in response to deblossoming and gibberellic acid. Proceedings of the Florida state Horticultural Society. 1997; 104:41-43.
45. National horticulture board, 2015.
46. Pal S, Ram S. Endogenous gibberellins of mango shoot-tips and their significance in flowering. Scientia Horticulturae. 1978; 9:369-379.
47. Peterson RH, Taber HG. Technique for vital staining of tomato pollen with fluorescein diacetate. Hort Science. 1987; 22:953.
48. Pongsomboon W. Effects of temperature and water stress on tree growth, flowering, fruit growth and retention of mango (*Mangifera indica* L.). Ph.D. thesis, Kasetsart University, Bangkok, Thailand, 1991.
49. Protacio CM, Restituto D, Bugante Jr., Julita Quinto, Gina Molinyawe, Gerry Paelmo. Regulation of flowering in Carabao mango trees by paclobutrazol. Philipp. J Crop Science Society of the Philippines. 2000; 25(1):27-33.
50. Randhawa V.K. Damodaran Studies on floral biology and sex ratio in mango (*Mangifera indica* L.) a review Ind. J Hort. 18, 1961, 29-45.
51. Rao MM, Srihari D, Patil VS. Further studies on chemical induction of flowering directly on fruited shoots in off phase Alphonso mango trees. Karnataka Journal of Agricultural Science. 1997; 10:598-601.
52. Reece PC, Furr JR, Cooper WC. Further studies of floral induction in the shoots and their relation with fruit-bud-differentiation. Hort. Adv. 1949; 4:48-59.
53. Singh RN. Studies in the differentiation and development of fruit buds in mango. II Morphological and histological changes. Hort. Adv. 1958; 2:37.
54. Singh RN. Studies in the differentiation and development of fruit buds in mango smudging and ethephon application. Hort. Science. 1960; 7:343.
55. Skoog F, Miller CO. Chemical regulation of growth and organ formation in plant tissues cultured in vitro. Symp. Soc. Exp. Biol. 1957; 11:118-130.
56. Whiley AW, Rasmussen TS, Saranah JB, Wolstenholme BN. Effect of temperature on growth, dry matter production and starch accumulation in tenmango (*Mangifera indica* L.) cultivars. Journal of Horticultural Science. 1989; 64:753-765.
57. Yeshitela T, Robbertse PJ, Stassen PJC. Effect of various inductive periods and chemicals on flowering and vegetative growth of Tommy Atkins and Ketti mango (*Mangifera indica*) cultivars. New Zealand Journal of Crop and Horticultural Sciences. 2004; 32:209-215.
58. Yeshitela T, Robbertse PJ, Stassen PJC. Potassium nitrate and urea sprays affect flowering and yields of Tommy Atkins (*Mangifera indica*) mango in Ethiopia. South African Journal of Plant. 2004.