Physiology of Mango (*Mangifera indica* L.) Flowering

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Summary

Mango flowering (*Mangifera indica* L.) is the first of several events that set the stage for mango fruit production on each year. The mangoes were takes place for mango bud to flower determined until after shoot initiation. Contemporary with shoot initiation, induction occurs based on the conditions present at the time of initiation. Floral induction of mango shoots under subtropical conditions strongly influenced by cool temperatures, although a period of low temperature (<18 °C) during the pre-flowering period. Studies with mango trees favour the survival of a florigenic promoter that is continuously induces mango flowering and synthesized in leaves. The studies of translocation propose that the florigenic promoter is movement from leaves in phloem facilitates transport to buds to induce flowering. Floral induction appears to be governed by the interaction of the vegetative and reproductive promoters. Under subtropical conditions, 1/4 leaf per stem caused 95% flowering of lateral shoots in 'Keitt' trees exposed to cool temperatures, and 1/2 or more of leaf per stem resulted in 100% reproductive shoots. In the tropical temperature conditions, floral induction occurs in stems that have achieved adequate time in rest since the previous shoot.

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Introduction

Mango (*Mangifera indica* L.), member of family Anacardiaceae, is amongst the most important tropical fruit of the world. It is also called as king of the fruits. Mango flowering is the first of several events that stage for mango production on each year. Flowering is an important physiological event that sets the start of mango fruit production. Mango flower thought to be determined by number of leaves, age of the last vegetative flush, environment or climatic factor. The flowering model conceptual has been described to explain the interaction of internal and external factors regulating vegetative and reproductive shoot initiation and induction in mango trees growing in tropical and subtropical environments. The model have been published elsewhere (Davenport and Nunez-Elisea, 1997; Davenport, 2000) and an updated account will soon be available (Davenport, 2007). Mango flowering can be operated in order to obtain off-season fruits and improve mango productivity. The purpose of this review is focus on the minimum number of leaves, translocation distance of the florigenic promoter and temperature on flowering.

Mango Phenology

Phenology is generally described as observation of the life-cycle phases of plants and relationship with the environment, especially climate. It involves invest irrigation of the response of living organisms to seasonal and climatic changes in the environment (Lambers*et al*., 1998). Mango passes through different phonological stages that start with cell division of apical and lateral meristems. Individual stems are dormant most of the time. Dormancy periods are short in young plants but can last more than 8 months between flowering and vegetative shoot episodes in mature trees (Davenport, 2000). Mango trees produce basically 3 types of shoots as a consequence of cell division such as vegetative shoots bear only leaves, generative shoots produce inflorescences, and mixed shoots produce both leaves and inflorescences within the same nodes (Fig. 1) (Davenport, 2007, 2009; Ramirez and Davenport, 2010).The frequencies of shoots that occur depend on cultivar, size of tree, and growing conditions (Davenport, 2000). The vegetative shoot development from initiation of growth to full elongation requires 3-6 weeks, depending on the cultivar and climatic conditions (Whiley *et. al*., 1991; Davenport, 2009). Vegetative shoots undergo distinct changes from early shoot development to maturation of leaves (Davenport *et al*., 2001). Nunez-Elisea *et al*. (1996) reported that the vegetative growth flushes occur during warm temperatures, around 25 °C under subtropical conditions. Flushes occurring during low temperatures of 5-15 °C usually produce flowering. Reproductive flushes generally occur after extended periods of stem rest in the low-latitude tropics often following a period of mild water stress or during cool inductive temperatures in the higher latitude tropics and subtropics (Davenport, 2000, 2003). Growth and development of mangoes is determined by climatic conditions (Galan-Sauco, 1999). In subtropical conditions with well-defined seasons, growth of mango canopy is typically synchronous with a time-gap between vegetative, rest and reproductive stages (Galan-Sauco, 1999; Davenport, 2009).Under tropical conditions growth and developments of mango is asynchronous sometimes displaying flowers, fruits and resting stems at the same time in different portions of the tree canopy (Davenport and Nunez-Elisea, 1997; Galan-Sauco, 1999; Davenport, 2009). Ramirez *et al.* (2010) indicated that reproductive and vegetative shoots occur synchronously throughout the canopy two times per year in the tropics of Colombia, South of America.

Fig. 1. Stylized display of shoot types found in mango.

Floral Initiation and Induction

The mango flowering is a key reproductive shoots incidence for the mango production. Shoots initiation in mango is the first event that takes place for mangoes to flower (Davenport and Nunez-Elisea, 1997; Davenport, 2000, 2003, 2009). Initiation is the onset of shoot development, regardless of the type of shoot evoked. It involves in cell division and elongation of dormant cells in leaf primordial (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 (Davenport, 2007; 2009). In contrast, Davenport (2009) considered that shoot initiation is stimulated by environmental factors, such as the change from dry to rainy season in the tropics and a shift from cool to warm temperatures. Initiation also can be stimulated by anthropogenic factors such as pruning, irrigation, application of nitrogen substances fertilizers and exposure to ethylene. Mango is a terminal bearing species and the factors which determine changing from vegetative to reproductive mode are poorly understood, although a period of low temperature (<18 °C) during the pre-flowering period is thought to be involved (Davenport and Nunez-Elisea, 1997). Shoot initiation in mango such as initiation of bud break, must happen before induction can determine the type of shoot to be evoked in those buds. They are different physiological events that lead to the formation of reproductive, vegetative, or mixed shoots (Davenport, 2007, 2009). Wilkie *et al.* (2008) indicated that many herbaceous plants are photoperiodic, that is they flower in response to day length. Photoperiod is sensed in the leaves, with long-day and short-day plants flowering in response to the change in the dark period, requiring short and long dark periods, respectively. Whereas, Nunez-Elisea and Davenport (1995) suggested a container-grown mango trees were exposed to photoperiods of 11, 12 or 13 h found that photoperiod had no effect on the vegetative or reproductive state of axillary buds in mango, and cool temperatures 18 °C day/10 °C night caused floral initiation.

The floral induction in mango is the temporary commitment of buds to evoke a particular developmental pathway (i.e. vegetative shoot, generative shoot or mixed shoot) when growth is initiated (Davenport, 2007; 2009). Coincident with shoot initiation, induction occurs based on the conditions present at the time of initiation (Davenport, 2000). Although conditions suitable for floral induction may be present before shoot initiation in tropical fruit trees, determination of the inductive conditions in buds is not made until initiation occurs (Batten and McConchie, 1995; Davenport and Nunez-Elisea, 1997; Nunez-Eliseaet *et al.*, 1993; 1996). Mango floral inductive may be present prior to bud initiation, it must be present at the time of initiation for flowering to occur (Kulkarni, 1988; Nunez-Elisea and Davenport, 1995; Nunez-Elisea *et al.*, 1996; Davenport and Nunez-Elisea, 1997; Davenport *et al.*, 2006).Floral inductive can be shifted from floral (F) to vegetative (V) or to vegetative to floral, F/V or V/F transition shoots, by altering temperatures during early shoot development (Fig. 1) (Batten and McConchie, 1995; Nunez-Elisea *et al.*, 1996; Davenport, 2009).

Florigenic and Vegetative Promoter

Florigenic promoters, induced by flowering stimuli and produces in the leaf are translocated to bud to stimulate floral initiation. The experiments explain how leaves are the site of synthesis of an unknown substance called 'florigen' or 'florigenic promoter' (FP) for more than 70 years (Aksenova *et al*., 2006; Zeevaart, 2006). The FP protein has been shown induce flowering in woody angiosperms (Bohlenius *et al*., 2006; Davenport, 2007; 2009). The existence of a FP that induces flowering such as citrus (Davenport, 1990), litchi (Davenport *et al*., 1999), mango (Davenport, 2009; Ramirez *et al*., 2010) and poplar (Bohlenius *et al*., 2006).The experiments of mango support the survival of a florigenic promoter which is continuously synthesized in leaves of mango at levels governed by temperature (Davenport and Nunez-Elisea, 1990, 1997; Davenport *et al*., 1995; Davenport, 2007; 2009). The mango found that a FP is synthesized in leaves during exposure to cool, floral inductive temperatures and moves to buds to induce flowering (Davenport and Nunez-Elisea, 1990; Davenport *et al*., 1995, 2006). The experiments of girdling indicated that the FP is translocated via phloem to apical buds (Nunez-Eliseaand Davenport, 1991; Nunez-Eliseaet *et al*., 1996; Davenport and Nunez-Elisea, 1997; Kulkarni, 1991; Davenport *et al*., 2006; Davenport, 2009). Studies with mango of shoots that were girdled to isolate them from the rest of the tree and completely defoliated produced only vegetative shoots, indicating that the FP is produced in leaves (Davenport and Nunez-Elisea, 1997; Nunez-Elisea *et al*., 1996; Ramirez *et al*., 2010).

Induction of reproductive or vegetative shoots from axillary or apical buds of mature shoots appears to be governed by the interaction of an age-dependent vegetative promoter and a temperature-dependent florigenic promoter (Davenport and Nunez-Elisea, 1997; Davenport, 2000; 2003; 2007; 2009). Under subtropical conditions, cool temperature not only triggers bud break but also favours higher ratios of florigenic promoter to vegetative promoter in developing buds (Nunez-Elisea and Davenport, 1995; Ramirez and Davenport, 2010).Induction in mango trees controlling the type of shoots that are evoked upon initiation, appears to be governed by the interaction of a temperature regulated florigenic promoter (FP) and an age dependent vegetative promoter (VP) (Davenport and Nunez-Elisea, 1997; Davenport, 2000; 2003; 2007; 2009). Irrespective of the endogenous levels of the individual components perceived in buds at the time of shoot initiation, floral and vegetative inductive responses can be effectively explained by the ratio of the FP and VP (Davenport, 2000; 2007; 2009). When the putative ratio of the FP and VP increases to a critical threshold level due to high FP as a result of low temperatures in the subtropics, or decreased VP levels in stems of advanced age compared with the basal level of FP in the tropics, it results in floral induction when shoots are initiated in stems. Overall, low FP/VP ratios may be conductive to induction of vegetative shoots, whereas high ratios when shoot initiation occurs may be conductive to induction of generative shoots, and at intermediate levels, mixed shoots are induced. The FP appears to be up regulated during exposure to cool temperatures below 18 °C in subtropical conditions; however, there appears to be a basal level present at all times regardless of temperature in order to regulate flowering during warm temperature conditions of the tropics (Davenport, 2000). In the tropical conditions, floral induction of initiating shoots usually occurs in terminal stems that have attained sufficient time in rest since the previous shoot of at least 4 or 5 months depending on the cultivar (Nunez-Elisea and Davenport, 1995; Davenport, 2003; Ramirez *et al*., 2010). Under warm conditions, the age of the last shoot of stems is the primary factor regulating floral induction. The older age of the last vegetative shoot and greater stem maturity, the more likely it is to flower when the next shoot occurs (Davenport, 2003). Ramirez *et al*. (2010) reported that cumulative stem maturity is conductive to induction of reproductive shoots in Colombia, South of America.

The putative VP stimulates vegetative shoots counteracting the influence of the florigenic promoter. The VP may be a gibberellin or closely associated with the gibberellin synthesis pathway as indicated by enhanced flowering responses of trees to plant growth retardants (Davenport, 2009). The GA biosynthesis in higher plants can be divided into three stages as (1) biosynthesis of ent-kaurene in proplastids (2) conversion of ent-kaurene to GAs 12 via microsomal cytochrome P450 mono oxygenase sand (3) formation of C 20- and C 19-GAs in the cytoplasm (Olszewski *et al*., 2002). Some enzymes for example, ent-kaurene oxidase (KO) and ent-kaurenoic acid oxidase are of major importance in these events and are the site of and of gibberellins biosynthesis by triazoles (Dalziel and Lawrence, 1984; Henry, 1985). Because triazoles inhibit the biosynthesis of gibberellins, they could reduce the influence of gibberellins rather than amplify the action of the putative florigenic stimulus in order to achieve the flowering response (Davenport and Nunez-Elisea, 1997). The putative VP appears to be most active in leaves of young stems and slowly dissipates over time to allow expression of the FP when shoots are initiated to grow in warm conditions (Davenport, 2009). Davenport (2007) indicated that the VP should be viewed as age dependent evidently decreasing mango mature leaves. The presence of an age-regulated VP in stems of mango interacting with the temperature-regulated FP best explains the induction of specific receptors by this promoter in leaf primordial of buds to cause development of leaves in vegetative or mixed shoots.

Temperature and Flowering

Mango flowering appears to be determined by a temperature conditions. Floral morphogenesis is initiated during cool weather in the subtropical and in the high altitude tropics region. Cool temperatures around 15 °C or lower promote inflorescence morphogenesis, whereas temperatures of around 20 °C or higher induce vegetative morphogenesis (Nunez-Elisea and Davenport, 1994; Nunez-Elisea *et al*., 1996). The effect of temperature is more evident under subtropical conditions where flower formation occurs during exposure to floral inductive cool temperatures (Davenport, 2009). Temperature is the most important factor where shoots are initiated. Nunez-Eliseaand Davenport (1991) suggested that temperature below 20 °C day/15 °C night will induce inflorescence development (Davenport and Nunez-Elisea, 1997; Robbertse *et al*., 2001). Floral or vegetative induction occurs when production of reproductive shoots requires initiation of growth during exposure to cool condition. The resting buds of plants, which had been exposed to cool temperatures (18°C day/10°C night) for more 3 weeks and then transferred to a warm temperature regime (30°C day/25°C night) before initiation occurred produce only vegetative growth. Yeshitela *et al*., (2004) found that 'Keitt' mango cultivar was more sensitive towards low temperature floral induction than the 'Tommy Atkins'. The reproductive and vegetative growth responses of several monoembryonic and polyembryonic cultivars to three temperature regimes ranging from vegetatively inductive (25 °C day/20 °C night) and (30 °C day/25 °C night) to flower inductive (15 °C day/10 °C night) (Whiley *et al*., 1989, 1991). Mango trees develop vegetative shoots when shoot initiation occurs in warm temperatures (30 °C day/25 °C night), whereas inflorescences develop when shoots initiate growth in cool temperature conditions (18 °C day/10 °C night; or 15 °C day/10 °C night) (Whiley *et al*., 1989; Nunez-Elisea and Davenport, 1995; Nunez-Elisea *et al*., 1993, 1996). Nunez-Elisea and Davenport (1995) reported that time of exposure to low temperature (18 °C day/10 °C night) and the minimum leaf age required by stems for floral induction was examined. The flowering response to temperature occurs in mangoes grown in the low latitude tropics rely less on low temperature for floral induction than trees grown in the high latitude tropics and subtropics (Davenport, 2009).

The Minimum Number of Leaves and Translocation of the Florigenic Promoter for Floral Induction

The minimum number of leaves necessary for mango flowering. Davenport *et al*. (2006) report that the number of leaves necessary to induce flowering in cool, subtropical conditions. Davenport *et al*. (2006) reported that during cool conditions, the requirement of leaves for floral induction and demonstrated that only 1/4 leaf per stem provided adequate FP to induce reproductive shoots in 95% of lateral initiating shoots in 'Keitt' mango stems floral inductive conditions. They also estimated the basal production levels of this putative FP in the warm tropics compared to up-regulated levels during the cool temperatures of the companion experiment conducted in South Florida. Davenport *et al*. (2006) suggested that 1/4 leaf per stem induced of 95% flowering of lateral shoots in 'Keitt' mango trees exposed to cool temperatures (night temperatures <13 °C), and 1/2 or more of leaf per stem resulted in 100% reproductive shoots. Ramirez *et al*. (2010) found that 1/4 or 1/8 leaves per stem, caused up to 11% flowering of lateral shoots in 'Keitt' mango trees in warm conditions (max-min temperatures are 26.6 and 18.1 °C, respectively) in La Mesa, Cundinamarca State, and 4-leaf per stem resulted in 22% reproductive shoots. Branches bearing 4 leaves per stem in 'Tommy Atkins' mango trees produced the maximum flowering with 45% reproductive shoots. The beginning level of FP in tropical conditions in Colombia vs. subtropical conditions in South Florida was calculated based on data obtained (Ramirez *et al*., 2010; Davenport *et al*., 2006). Ramirez and Davenport (2010) report that at La Mesa, have an estimated 3% of FP per leaf in 'Keitt'mango trees exposed to warm compared to cool temperatures. Such comparisons provide direct evidence supporting the theory that the FP is produced at substantially lower percentage in warm temperatures than in cold temperatures. FP is synthesized in leaves under cool temperature conditions than during warm tropical conditions with a lower basal level of FP (Davenport, 2000). The mango experiments have long supported the existence of a florigenic promoter in leaves of mango and moves to buds to induce flowering during exposure to cool temperature (Davenport *et al*., 1995, 2006; Davenport, 2009; Ramirez *et al*., 2010). The FP has been shown to be synthesized in leaves and transported to buds via phloem based on the observed requirement of leaves for mango flowering (Davenport *et al*., 2006; Davenport, 2009). Davenport *et al*. (2006) result indicated that during periods in cool condition, floral inductive at night temperatures (<13 °C), proved movement of the florigenic promoter from donor stems bearing 1-5 leaves to induce flowering in initiating buds, receiver stems borne on two limbs of bifurcated branches. The branches with designated donor stems bearing no leaves produced only vegetative shoots on the donor and in all receiver stems. The branches with donor stem bearing five leaves consistently initiated 100% flowering shoots in the donor and receivers stem. Davenport *et al*. (2006) reported that the leaves numbers on the donor stems illustrated a pattern of decreasing proportions of reproductive shoots and with increasing distance of receiver stems from the donor stems. This movement was determined to reach more than 100 cm from one stem to another along branches under cool, floral inductive subtropical conditions. Subtropical conditions in Florida, results of experiments in warm tropical conditions in Colombia (Ramirez *et al*., 2010) provided supporting evidence that the mango florigenic promoter can move considerable distances in 'Tommy Atkins' branches even during warm, tropical conditions. Floral induction occurred in initiating shoots on stems located up to 52 cm from the 5-leaf donor stem, but the amount of the FP was not adequate to induce reproductive shoots in the fourth and fifth receivers, which were induced to be vegetative and located as much as 67 and 87 cm from the donor respectively. Davenport *et al*. (2006) reported that five leaves on the donor stems induced an average of 38% reproductive shoots among all of the donors and receiver stems in 'Tommy Atkins' mango trees under subtropical condition.

Conclusion

Mango flowering is an important physiological event that sets the star of fruit production. Mango under subtropical and high-latitude tropical conditions induce flowering by cool temperatures. Mango is a terminal bearing species and the factors which determine switching from vegetative to reproductive shoots are poorly understood, although a period of low temperature (<18 °C) during the pre-flowering period is thought to be involved. FP production depend on leaves, they are essential for mango flowering. One quarter of leaf per stem provided sufficient FP to induce flowering in 95% of initiating lateral shoots and 1/2 or more of leaf per stem resulted in 100% reproductive shoots in under subtropical conditions. In tropical conditions, the 1/4 or 1/8 of leaf surface only induced flowering in an average of up to 11% of initiating lateral shoots. Translocation of the FP was greater, due to larger per leaf numbers, in subtropical condition compared to tropical condition.

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芒果(*Mangifera indica* L.)開花生理之研究

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關鍵字：花芽分化、花芽誘導、開花基因啟動子、芒果開花

摘要：芒果開花是每年果實產生的重要過程。芒果的芽變成花取決於芽的分化，在花芽分化的同時，花芽誘導也隨著發生。在亞熱帶氣候下，芒果花芽的誘導受低溫影響，特別是開花前需經過一段低溫(＜18°C)，前人研究指出，芒果有開花基因啟動子的存在，在葉片中合成會持續的誘導芒果開花，轉錄學說指出，開花基因啟動子會經由葉片移動到韌皮部，並運送到芽以誘導開花，花芽誘導受營養生長和生殖生長之間啟動子相互作用所控制。在亞熱帶氣候下，'凱特'芒果經低溫，每個莖留1/4片葉子即可促使95%側芽開花，而1/2或更多的葉片導致100%的開花。在熱帶地區，發育充實且具充足休眠之前一季枝條才可成功誘導花芽。

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