Reproductive physiology of mango

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Mango flowering involves hormonal regulation of shoot initiation and induction events resulting in reproductive shoot formation. A balance or ratio of endogenously regulated phytohormones, thought to be auxin from leaves and cytokinins from roots, appears to govern the initiation cycle independently from inductive influences. Induction of reproductive or vegetative shoots is thought to be governed by the ratio of a temperature-regulated florigenic promoter and an age regulated vegetative promoter at the time of shoot initiation. Management of off-season flowering in mango trees is being accomplished in the tropics by successfully synchronizing shoot initiation through tip pruning and 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.
Key words: auxin, cytokinin, flowering management, fruiting, hormones, *Mangifera indica*

Fisiologia da reprodução em manga: A floração em manga envolve regulação hormonal de iniciação dos ramos e eventos indutivos que levam à formação de ramos reprodutivos. Um equilíbrio ou uma relação entre fito-hormônios regulados endogenamente, supostamente auxinas das folhas e citocininas das raízes, parece governar o ciclo de iniciação independentemente de influências indutivas. Acredita-se que a indução de ramos vegetativos ou reprodutivos é governada pela relação entre um promotor florigênico regulado por temperatura e um promotor vegetativo associado à idade, durante a iniciação do ramo. Nos trópicos, o manejo da floração fora da estação das floradas tem sido feito com sucesso, pela sincronização da iniciação de ramos, mediante a remoção do ápice e uso de pulverizações com nitrato, em associação com manejo da idade do caule para induzir a floração, o que pode ser executado em qualquer época do ano.
Palavras-chave: auxina, citocinina, frutificação, hormônios, manejo da floração, *Mangifera indica*

INTRODUCTION

Flowering is the first of several events that set the stage for mango (*Mangifera indica* L.) production each year. Given favorable growth conditions, the timing and intensity of flowering greatly determines when and how much fruit are produced during a given season. Insight into this phenomenon has been of prime interest to scientists and growers for over a century. As a consequence of efforts to elucidate the mechanisms of this critical biological event in mango and other model plant systems, many of the important details are becoming clearer at the molecular, biochemical, and physiological levels resulting in a better understanding of how to manage flowering in the field. A conceptual flowering model (Figure 1) 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. Details of this model have been published elsewhere (Davenport and Núñez-Eliséa, 1997; Davenport, 2000) and an updated account will soon be available (Davenport, 2008). This review will briefly summarize the basic mechanisms of mango shoot formation, discuss recent advances in our knowledge of floral induction, and focus on how this information can be utilized to control reproductive and vegetative growth of this crop.

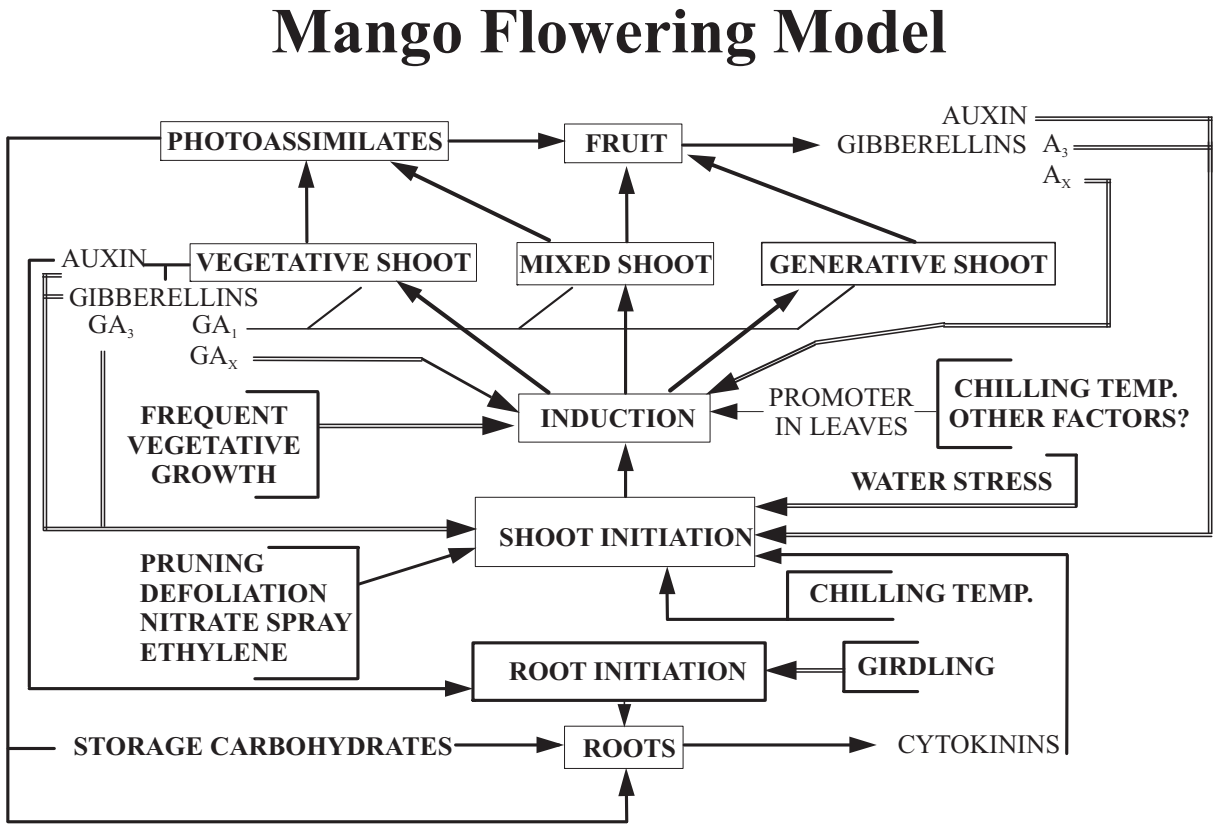

Figure 1. Conceptual flowering model of mango. The model summarizes the proposed roles for various phytohormones in initiation of shoot growth and in defining the vegetative or reproductive outcome of that growth (induction). Single lines in the scheme are promotive and double lines are inhibitory.

PHYSIOLOGY OF MANGO FLOWERING

Individual stems borne on branches of mango trees are in rest or a quiescent mode most of the time. Stems are resting, vegetative structures composed of the terminal intercalary unit resulting from the previous flush of vegetative growth (Davenport and Núñez-Eliséa, 1997). 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 (Figure 2). Ephemeral episodes of vegetative shoot growth occur periodically from the apical or lateral buds of stems and last about two weeks before these shoots then go into the resting state to become the new terminal stems. These episodes are called flushes if they occur on many stems and branches. There may be several flushes of vegetative shoots per year, but flushes of reproductive shoots usually occur only once per year on individual stems. If synchronized, the flush will occur at once in all stems throughout the canopy. More often than not, however, growth flushes occur in sections of canopy instead of the whole in trees grown the tropics, and hence may produce reproductive shoots in one section on one occasion during the flowering season and in other sections on other occasions until the entire canopy has flowered.

Initiation of shoot growth in buds of resting stems is the first event that must occur in order to produce flowering (Davenport and Núñez-Eliséa, 1997; Davenport, 2000, 2003, 2008). Initiation is the onset of shoot development, regardless of the type of shoot evoked. It commences with the first events involved in cell division and elongation of dormant cells specifically in leaf primordia (vegetative shoots), axillary meristems (generative shoots) or both (mixed shoots), followed soon thereafter by cell divisions in the apical meristem. These secondary cell divisions produce more nodes comprised of leaf primordia and lateral meristems, which

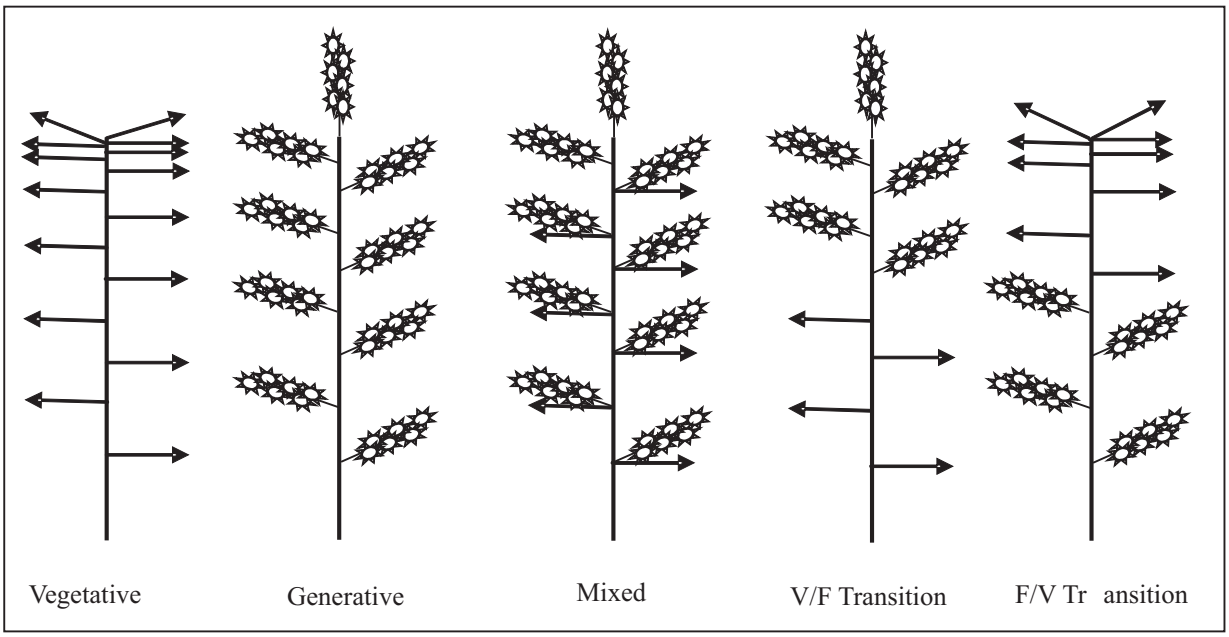

Figure 2. Stylized display of shoot types found in mango. Arrow (⟶) represents individual leaves, and floral diagram ( ) represents lateral inflorescences.

then give rise to the distal portion of the developing shoot. Shoot initiation is stimulated by pruning, defoliation, irrigation during dry conditions, application of nitrogen fertilizer, and other factors, e.g., exposure to ethylene or a shift from cool to warm temperatures. Reece et al. (1946, 1949) recognized that the fate of mango buds is not determined until their growth is initiated. Others have also noted that the vegetative or reproductive fate of resting apical or lateral mango buds is not predetermined at the time of shoot initiation (Mustard and Lynch, 1946; Núñez-Eliséa and Davenport, 1992; Davenport et al., 2006a). This characteristic differs from some temperate fruit trees in which previously initiated floral buds become dormant to over-winter before being evoked in the spring (Sedgley, 1990; Westwood, 1993; Greene, 1996). Reece et al. (1949) also realized that a putative signal, which triggers initiation of shoot development, is separate and different from the inductive signal that determines the fate of the shoot. Removal of apical buds by pruning stimulates initiation of axillary shoots in lateral buds (Reece et al., 1946, 1949; Singh and Singh, 1956; Núñez-Eliséa and Davenport, 1992; Núñez-Eliséa et al., 1996). Defoliation of the apical whorl of five to 10 leaves also stimulates shoot initiation in dormant apical buds (Núñez-Eliséa and Davenport, 1995). The shoots that emerge in response to these initiation stimuli, however, are determined by other factors unrelated to initiation and which are prevalent at the time that initiation occurs. Light pruning in the subtropics, for example, during warm the summer months results in initiation of vegetative shoots from axillary buds, whereas pruning during cool winter months usually results in initiation of axillary inflorescences.

Induction is the temporary commitment of buds to evoke a particular shoot type, i.e. vegetative shoot (vegetative induction), generative shoot (floral induction) or mixed shoot (combined vegetative-floral induction) in initiating shoots. This definition differs from that developed from herbaceous plant flowering models (Bernier et al., 1981, 1993; Halevy, 1985-1986; Bernier, 1988; Huala and Sussex, 1993; Kinet, 1993). In those flowering models, a critical photoperiod or vernalization treatment or both, induces production of a floral stimulus. This stimulus causes an irreversible shift in the mother cells of the apical meristems from producing transcripts responsible for organizing and developing subtending vegetative structures to initiation of those responsible for development of reproductive structures.

Whereas the floral inductive signal in mango may be present prior to initiation, it must still be present at the time of shoot initiation for flowering to occur (Kulkarni, 1988a; Davenport, 1993; Núñez-Eliséa and Davenport, 1995; Núñez-Eliséa et al., 1996). In addition, the inductive signal can be shifted from reproductive to vegetative or vegetative to reproductive by altering temperatures to which the plants are exposed during early shoot development (Núñez-Eliséa et al., 1996). This treatment produces reproductive-to-vegetative (R-V) transition shoots or vegetative-to-reproductive (V-R) transition shoots, respectively (Figure 2). The distinctly different morphogenic responses to altered conditions clearly demonstrates the plasticity of induction, indicating that cells of the apical meristem do not become irreversibly determined when placed in inductive conditions even though nodal tissues are proceeding to their determined fate to produce vegetative or reproductive shoots. These results suggest that the apical meristem provides the progenitor cells, some of which later differentiate into specific target cells at each node in the apex. The mango apical meristem may, therefore, not be directly involved in the flowering process (Davenport and Núñez-Eliséa, 1997; Davenport, 2008).

The target cells, by virtue of their location in buds within each node, are competent to respond to the inductive signal. Target cells, located in leaf primordia or lateral meristems may independently become activated to proceed on a genetically predetermined course. When initiated to grow under vegetatively inductive conditions, individual leaf primordia develop into leaves and subtending lateral meristems associated with each developing leaf organize to form dormant lateral buds with protective bracts. The lateral buds can develop in subsequent flushes into vegetative shoots when initiated in vegetatively inductive conditions or into axillary inflorescences during floral inductive conditions as described above. In strongly floral inductive conditions that give rise to generative shoots, however, leaf primordia fail to develop beyond the bract stage before becoming dormant. Each lateral meristem organizes to form nodes consisting of primordial leaves and lateral meristems, but development of these meristems is influenced by the presence of a putative floral-inductive stimulus so that floral structures are formed which terminate in cymose inflorescences borne on each tertiary peduncle (Davenport, 2008). Such development has been attributed to cascades of sequentially activated floral identity genes, which in the case of mango would result in the development of floral structures borne on each primary peduncle (Weigel et al., 1992; Coen and Carpenter, 1993; Lumsden, 1993; Yanofsky, 1995). Formation of the primary, secondary and tertiary peduncles, as well as pedicels of inflorescences is always accompanied by a subtending bract or vestigial leaf at each node. Shoot initiation during weakly floral-inductive conditions activates growth of both the leaf primordia to develop leaves and the lateral meristems to produce peduncles bearing inflorescences, thus, forming mixed shoots.

Shoot initiation is driven by different factors than those regulating induction events that determine whether the developing shoots will be vegetative or reproductive. It is thought to involve the interactive ratio in buds of accumulated cytokinins from roots with declining auxin production and transport from leaves of increasing age (Figure 1; Davenport and Núñez-Eliséa, 1997; Davenport, 2000, 2003, 2008). Frequent flush events occur in young trees and in mature trees in conditions of high nitrogen and abundance of water. Other factors that stimulate initiation of shoot development include stem pruning, defoliation, foliar nitrogen sprays, and ethylene. Induction, controlling the type of shoots that are evoked upon initiation, appears to be governed by the interaction of a putative temperature-regulated florigenic promoter (FP) and an age-dependent vegetative promoter (VP) (Davenport and Núñez-Eliséa, 1997; Davenport, 2000, 2003, 2008).

The FP appears to be up-regulated during exposure of leaves to cool temperatures and down-regulated to a constant basal level when temperatures are warm (Davenport, 2000). In contrast, the VP is thought to gradually decrease within leaves or buds as stems age, impacting the fate of initiating buds up to about four months after the young, limp-red-leaf stage of development. The ratio of FP to VP in buds, not the absolute concentration of either, is thought to induce formation of the distinct shoot types; i.e., high FP to VP ratio induce generative shoots, low FP to VP ratios induce formation of vegetative shoots, and intermediate FP to VP ratios may be responsible for formation of mixed shoots (Davenport and Núñez-Eliséa, 1997; Davenport,

2000, 2003, 2008). For example, floral induction of initiating shoots during exposure of trees to cool, subtropical temperature conditions is considered to be the result of elevated levels of up-regulated FP. High VP levels in young stems, however, may counterbalance the impact of FP, such that exposure to cool temperatures at the time of shoot initiation causes vegetative shoot induction despite the presence of cool temperatures. Thus, floral induction in the subtropics is primarily driven by the intensity and duration of cool temperatures, but increasing age of the previous vegetative flush positively moderates the response.

Temperatures rarely go below 18º C to 20º C in the low-latitude, humid tropics; hence, the FP is thought to be produced at a constantly low, basal level in order to induce flowering. Mango flowering only occurs in tropical warm temperatures in initiating shoots of stems that have achieved sufficient age since the previous vegetative flush, i.e. four to five months depending upon cultivar (Davenport, 2003). Recent experimental results have quantitatively confirmed this observation in the Dominican Republic (T.L. Davenport and J. Oleo, unpublished data) and in Colombia (F. Ramirez and T.L. Davenport, submitted for publication). Evidence indicates that, in order to induce flowering in warm conditions, the level of putative VP must drop to sufficiently low levels with stem age to raise the FP to VP ratio when compared to the proposed low level of the FP. Thus, flowering in the tropics is primarily regulated by the age of the previous vegetative flush and positively modified by cool temperatures in high elevations or areas where annual cool fronts can penetrate to reduce temperatures (Davenport, 2003).

Studies with mango have long supported the existence of a FP in mango leaves during exposure to cool, floral inductive temperatures (Reece et al., 1946, 1949; Singh, 1962, 1977; Núñez-Eliséa and Davenport, 1989, 1992; Davenport and Núñez-Eliséa, 1990; Davenport et al., 1995). Complete defoliation of girdled branches during inductive conditions results in vegetative shoots instead of generative shoots (Reece et al., 1949; Sen et al., 1972; Núñez-Eliséa and Davenport, 1989, 1992; Núñez-Eliséa et al., 1996). Davenport et al. (2006a) recently confirmed this requirement of leaves for floral induction but also demonstrated that only ¼ leaf per stem provided sufficient FP to induce reproductive shoots in 95% of lateral shoots initiating in deblossomed 'Keitt' mango stems during cool, floral inductive conditions. In contrast, similar experiments recently conducted during warm temperature conditions in the Colombian tropics revealed that as many as four leaves per stem in 'Keitt' trees resulted in only 22% flowering of initiating lateral shoots (F. Ramirez and T.L. Davenport, submitted for publication). The estimated relative amount of FP in warm leaves was about 2.5% that of leaves in the cold conditions.

Recent advances in molecular biology of flowering in the facultative, long-day, model herbaceous plant, *Arabidopsis thaliana*, [reviewed in Zeevaart (2006) and Aksenova et al. (2006)] has provided new insights into the nature of the floral stimulus. Activation of the *CONSTANS (CO)* gene encodes a protein, which in turn induces expression of the *FLOWERING LOCUS T (FT)* gene localized in phloem tissue in vascular veins of leaves. The protein product of FT acts as the florigenic component, that is translocated to *Arabidopsis* buds (Corbesier et al., 2007). This conclusion is supported by translocation from leaves to buds of an analogous protein encoded by Hd3a, a rice ortholog of FT, which appears to be the florigen operating in that crop (Tamaki et al., 2007), and the aspen ortholog, *PtFT1*, which along with *CONSTANS* was demonstrated to regulate the timing of flowering and growth cessation of *Populus trichocarpa* (Bohlenius et al., 2006). Once translocated to buds, the protein product of FT is thought to combine with the bZIP transcription factor (FD) protein to activate transcription of floral identity genes, such as *APETALA1 (AP1)* to begin floral expression (Abe et al., 2005; Wigge et al., 2005). Similar mechanisms may be active in mango but with greatly altered dynamics of gene expression.

Zhang et al. (2005) and Davenport et al. (2006b) isolated a *CONSTANS*-like gene (*MiCOL*) from mango leaf DNA by a combination of genomic walking and PCR methods. *CONSTANS* is a circadian expression gene interacting with the photoperiodic pathway in *Arabidopsis* (Putterill et al., 2004). This gene is central to activation of the FT gene in *Arabidopsis* during long days, but because mango is non-photoperiodic, the role of this gene in mango flowering systems remains unclear. The mango ortholog has 79%, 76%, and 62% homology with two apple *CONSTANS* genes, *MdCOL2* and *MdCOL1*, and the *Arabidopsis CONSTANS* gene *(AtCO)*,

respectively. Efforts to isolate the FT or homologous gene responsible for synthesis of the protein, FP, however, have, thus far, been unsuccessful.

The mango FP can be transported over long distances from leafy branches to defoliated branches that have not been girdled during cool temperature conditions (Sen et al., 1972; Núñez-Eliséa et al., 1996). Davenport et al. (2006a) demonstrated that the amount of FP available from ½ leaf on a donor stem in cool conditions was sufficient to induce flowering in an average of 50% of shoots emerging on the donor stem and five leafless receiver stems inserted increasing distances along isolated 'Keitt' mango branches. The average maximum distance traveled by the FP from the donor stem to receivers was more than 100 cm. Five leaves in the donor stem saturated the system with 100% generative shoots forming on all receiver stems whereas no leaves in the donors caused only vegetative shoots to form on the donors and receivers. Intermediate numbers of leaves (3, 1, ½) on the donor stem displayed decreasing proportions of reproductive shoots with both decreasing number of leaves on the donor and increasing distance of the receiver stem from the donor. Receiver stems that were inserted into the branch in the same orthostichy as the one donor leaf produced nearly 100% generative shoots. In contrast, shoots that initiated on those receiver stems that were inserted in the opposing orthostichy were predominantly vegetative. It was concluded that sugars made in the donor leaves was the driving force moving the FP in phloem from leaves to receiver stem buds. Shading experiments to reduce photosynthate loading into the phloem also support this view (Kulkarni, 1991; R. Núñez-Eliséa, T. L. Davenport and B. Schaffer, Florida, 1991, unpublished results). The reduction of about 90% sunlight onto leaves of girdled branches on field-grown trees resulted in reduced flowering of those branches during cool, inductive periods; however, complete shading, which stopped photosynthate production entirely, mimicked defoliation during inductive conditions, resulting in a vegetative growth response. The results of these experiments indicate that the mango FP, like the FT florigenic protein described in *Arabidopsis* (Corbesier et al., 2007) moves with photoassimilates in phloem from the donor leaves to buds in the receiver stems. This conclusion is borne out in donor-receiver experiments recently conducted in the warm tropics of Colombia, but the 'Keitt' mango apparently produced insufficient FP to induce flowering in both donor and receiver stems (F. Ramirez and T.L. Davenport, submitted for publication). 'Tommy Atkins' mango, however, demonstrated translocation of the limited amount of FP from donor steams to the nearest three receiver stems.

The FP is short-lived *in situ*, its influence only lasting 6 to 10 d (Núñez-Eliséa and Davenport, 1989, 1992; Núñez-Eliséa et al., 1996). Leafless cuttings taken from trees during cool inductive conditions produced inflorescences when stimulated to grow within 8 d of transfer to warm, non-inductive, temperature-controlled conditions. The same cuttings initiated only vegetative shoots after that time (Davenport et al., 1995). The measured time to deplete the active levels of FP in buds of isolated mango stems taken from trees exposed to cool floral inductive temperatures was 7 d after defoliation in warm (25°C night / 30°C day) conditions and 13 d in cool (10°C night / 18°C day) temperature conditions (Davenport et al., 2001; Davenport et al., unpublished). Thus, there is a constant turnover of the putative mango FP protein maintained by synthesis of new FP in leaves and deletion in buds.

The floral stimulus is also graft transmissible (Singh, 1959, 1962; Kulkarni, 1986, 1988b, 1991, 2004). Early flowering of seedling stems was stimulated by grafting them onto mature trees or by grafting the mature stems onto juvenile plants (Singh, 1959). Similar results were obtained by approach-grafting seedling plants to mature trees (Singh, 1962). Some mango cultivars selected in the tropics can flower at higher temperatures than others and are not restricted to winter flowering (Kulkarni, 1991). Transfer of the FP from tropical selections to those requiring lower temperatures for induction has been accomplished using reciprocal grafts between these cultivars (Kulkarni, 1986, 1988b, 1991). Cultivars that seldom flower in warm temperature conditions were made to flower in the off season using these techniques. Three conditions were essential for summer flowering to occur in the low-temperature-requiring cultivars (receptors) when grafted to the summer flowering type (donors): (a) the summer-flowering donor cultivar stocks or scions were in a flowering cycle, (b) buds on the receptor scions or stocks of grafted plants had initiated shoot growth during this cycle, and (c) receptor stocks or scions had

been completely defoliated for transfer and/or expression of the floral stimulus. The presence of any leaves providing the VP on receptor plants resulted in vegetative growth.

The VP may be a gibberellin or closely associated with the gibberellin synthesis pathway. Mangoes growing in wet and humid, low-latitude tropics, where night temperatures rarely fall below 18ºC, tend to produce frequent vegetative shoots and flower sporadically, perhaps due to higher levels of the VP in the young stems combined with low levels of the putative FP when shoot initiation occurs. Paclobutrazol, sold in the tropics under the trade name Cultar (Syngenta Corp., also available from several Chinese manufacturers and distributors), reduces the time in rest necessary to allow floral induction during warm temperature conditions by approximately one month (Davenport, 2003), thus increasing the potential to produce reproductive shoots in younger stems upon shoot initiation. Application of paclobutrazol or uniconazole [Sumitomo Chemical Co. (international) or Valent Corp. (USA)], triazole compounds that inhibit synthesis of kaurene oxidase in the gibberellin-synthesis pathway (Dalziel and Lawrence, 1984; Rademacher, 1991), stimulates production of flowering shoots during these weakly inductive conditions (Burondkar and Gunjate, 1991, 1993; Tongumpai et al., 1991; Voon et al., 1991; Nartvaranant et al., 2000; Yeshitela et al., 2004). Thus, field application of paclobutrazol to trees bearing one-month-old mango stems produced inflorescences from those stems when bud break was initiated three months later by a foliar application of KNO_3 (Davenport, 2003).

From this assessment, we assume that triazoles shorten the age requirement wherein the concentration of a specific gibberellin decreases as stems mature. Vegetative or reproductive induction at the time of shoot initiation appears to be governed by the ratio of the putative floral promotive and inhibitory components, as proposed in several plant species by Lang et al. (1977), Bernier et al. (1981), Lang (1984), Kulkarni (1988a) and Kondoh et al. (1999). In the case of mango, the floral inhibitor should be viewed as an age-dependent VP. Because triazoles inhibit the biosynthesis of gibberellins and stimulate early flowering of mango, it is most likely that the putative VP, perhaps itself a gibberellin, is reduced with the products of the gibberellin pathway.

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 target tissues (leaf primordia) of buds to cause development of leaves in vegetative or mixed shoots. A gradual decrease in the level or influence of the VP best explains the natural occurrence of vegetative shoots when initiation occurs on two-month-old stems and generative or mixed shoots when initiation occurs in stems from four to 6 months of age, given the constantly warm daily temperatures maintaining a constantly low level of FP in both situations. Finally, the floral promotive influence of triazole plant growth retardants suggests that the VP is closely linked to the gibberellin synthesis pathway.

Vegetative flushes typically occur one to many times per year on individual stems, depending upon, cultivar, age of the tree, and growing conditions. Reproductive flushes generally occur after extended periods of stem rest in older trees growing in the low-latitude tropics, often after relief of extended periods of non-lethal water stress (Núñez-Eliséa and Davenport, 1994), or during cool winter months in the higher latitude tropics and the subtropics. Control of mango flowering outside of these natural flowering times focuses on management of shoot initiation at a time when the ratio of these two putative promoters is favorable for flowering.

MANAGEMENT OF MANGO FLOWERING

Mango is one of the most amenable of the tropical fruit trees to floral manipulation. Producers are most interested in reliable out-of-season flowering in order to provide fruit for markets at times of maximum value. Flowering is not an important issue for commercially produced mangos in subtropical climates unless there is concern for reduced productivity through reduced flowering as a result of recent pruning. Flowering in tropical latitudes is, however, an important issue, both for dependable flowering and for manipulation of the timing of flowering to take advantage of market opportunities.

Most mango producers are interested in managing the flowering time of orchards in order to obtain early harvest. Mango prices are highest during March and April in today's markets in the northern hemisphere, and it takes about four months from flowering to fruit

maturity; hence, the normal February flowering period must be shifted forward in time to October in order to accomplish harvest during this most profitable time period. Because cool Arctic or Antarctic winter air rarely pushes deep into low altitude, tropical latitudes, flowering in these regions is not governed by winter-summer cycles of low temperature, as are the subtropical zones, which include south Florida and northern Mexico. The critical component regulating floral induction of mangoes in the tropics is the age of the last flush (Núñez-Eliséa and Davenport, 1995; Davenport and Núñez-Eliséa, 1997, Davenport, 2000, 2003, 2008). The older the age of the last vegetative flush (terminal intercalary unit), the more likely it is to flower when the next flush occurs. Some cultivars, such as 'Haden', 'Keitt', 'Kent', and 'Irwin' require less time in rest than do others, such as 'Tommy Atkins'. Young trees and trees receiving high rates of nitrogen fertilizer in moist conditions frequently initiate shoots resulting in vegetative shoot induction due to the short periods of stem rest between flushes. Successful floral management in the tropics, thus, requires discouraging initiation of shoots before the resting stems have reached sufficient maturity to induce flowering shoots.

There are distinct operations that one can accomplish to prepare mango trees for flowering at any time of the year utilizing the basic concepts discussed in the first part of this chapter. They must be performed at specific times in order for a flowering program to be successful on an annual basis. The flowering program can be started at any time regardless of the presence or absence of fruit. Other factors, however, such as harvest of the previous season's crop, timing of the dry and wet seasons, and high susceptibility of flowers and fruit to disease during rainy seasons, are important considerations when deciding on the starting date of the flowering program.

Synchronization of the vegetative growth of tree canopies in an orchard is a necessary first step in the flowering management program. Synchronous growth throughout each tree allows all of the stems in the canopy to be in the same physiological stage of maturity so that management can be most efficiently achieved uniformly throughout a section of orchard. Synchronized growth is best accomplished by tip pruning all of the stems on the trees (Tables 1 and 2). Tip pruning, thus, becomes the first operation to begin an annual flowering program. It not only causes a uniform flush of growth throughout the canopy, it removes growth – and flower – inhibiting factors in stems derived from the previous season's flowering and fruiting panicles (Davenport, 2006). Tip pruning also stimulates lateral shoot development forming five to 10 times the original number of productive stems, thus, increasing potential yield. It is essential that trees have adequate water at the time of pruning to facilitate a rapid flushing response because even mild water stress during the tropical dry season discourages shoot initiation.

Deeper level pruning to shape trees, such as cutting branches larger than 2 cm in diameter, usually results in a second vegetative flush occurring about three months after the first. It is essential that there be only one flush of vegetative growth that occurs about one month following the synchronizing prune (Davenport, 2006). The depth of the pruning cut, management of fertilizer (through monitoring of leaf nitrogen levels) during the wet season, and management of water during the dry season are important factors governing the probability of a second, undesirable flush occurring before the desired time of floral stimulation (Davenport, 2003). All three factors interact to promote or discourage an early second

Table 1. Mango flowering program without use of paclobutrazol or uniconazole for early floral stimulation of an easily induced cultivar (Haden) and a more difficult cultivar (Tommy Atkins). Schedule assumes rapid flush response one month after the synchronizing tip prune (SP).

Months From Synchronizing Prune for *'Haden'*												
0	1	2	3	4	5	6	7	8	9	10	11	12
↑SP					↑NO_3^-	↑Flowering				↑Harvest		
Months From Synchronizing Prune for *'Tommy Atkins'*												
0	1	2	3	4	5	6	7	8	9	10	11	12
↑SP						↑NO_3^-	↑Flowering				↑Harvest	

Table 2. Mango flowering program using paclobutrazol or uniconazole (P) for early flowering of an easily induced cultivar (Haden) and a more difficult-to-induce cultivar (Tommy Atkins). Schedule assumes rapid flush response one month after the synchronizing tip prune (SP).

Months From Synchronizing Pruning for *'Haden'*												
0	1	2	3	4	5	6	7	8	9	10	11	12
↑SP	↑P			↑NO_3	↑Flowering				↑Harvest			
Months From Synchronizing Pruning for *'Tommy Atkins'*												
0	1	2	3	4	5	6	7	8	9	10	11	12
↑SP		↑P			↑NO_3	↑Flowering				↑Harvest		

flush. Reducing the negative impact of one factor is usually sufficient to prevent occurrence of the second flush when given ample presence of the other two. For example, reducing water availability such that the plants are under mild water deficit cause trees to flush only once following pruning regardless of depth of pruning or nitrogen levels. Similarly, reduction of leaf nitrogen levels discourages a second flush during rainy seasons. Nitrogen fertilizer should never be applied near the time of pruning to reduce risk of second flushes before the stems have achieved sufficient maturity.

The next step in a mango flowering management program is to decide whether to use paclobutrazol or not. The triazole plant growth retardants, paclobutrazol (Cultar, Zeneca Corp.) and uniconazole (Sumitomo or Valent Corp.), are inhibitors of gibberellin biosynthesis (Rademacher, 1991); therefore, they reduce the levels of the putative vegetative promoter, thought to be a gibberellin. Both products are effective for assisting in floral induction with uniconazole being more effective than paclobutrazol. Both products are expensive, and they can cause permanent stunting of flushes if trees are severely pruned at any time after soil application (Davenport, 1994). For these reasons, they are not recommended for use to stimulate flowering in an annual flowering program; however, they do provide a strong measure of certainty that flowering will occur, when used properly, by shortening the time required between the synchronizing pruning and application of floral-stimulating nitrate sprays (Table 2) (Tongumpai et al., 1991; Voon et al., 1991; Nartvaranant et al., 2000). The triazole products provide the flexibility needed to shift the flowering time of the more-difficult-to-manage cultivars like 'Tommy Atkins' to any week of the year with less concern for early vegetative flushes. For this reason, Cultar has been widely marketed throughout the tropics to stimulate mango flowering.

Either product should be applied after the onset of re-growth following pruning (1-1.5 months after prune date) depending upon cultivar. Paclobutrazol should be applied in a soil drench containing 1 to 1.5 grams of active ingredient per meter of canopy diameter (Nartvaranant et al., 2000) if applied during the rainy season, but personal experience has shown that about half that amount is needed if applied during the dry season. It takes at least 90 d for either product to exert an effect in trees (Nartvaranant et al., 2000). Earlier initiation of flushes results in formation of vegetative shoots so it is still important to avoid growing conditions that promote initiation of frequent flushes when utilizing paclobutrazol.

More time must pass after pruning before stimulating flowering if paclobutrazol is not used (Table 1); however it is less costly and, if done properly, is just as reliable as using paclobutrazol but without the dangerous risk of permanently losing production in the orchard. It is easier to stimulate flowering of 'Haden', 'Keitt', 'Irwin', or 'Kent' due to the fact that the stems become sufficiently mature to elicit a floral response about five months after pruning in these cultivars. In contrast, 'Tommy Atkins' is more difficult to stimulate to flower in the American tropics. This is due to the added month of rest necessary prior to eliciting a flowering response (Tables 1 and 2).

Nitrate salts applied to foliage stimulate shoot initiation (Davenport and Núñez-Eliséa, 1997; Davenport, 2000, 2003, 2008). Floral stimulation with nitrate application must be accomplished at the time periods indicated in Tables 1 and 2, depending upon cultivar, night temperatures at the time, and upon whether

paclobutrazol is being utilized or not. Application of nitrate earlier than recommended usually results in vegetative instead of flowering flushes (Davenport, 2006). Any nitrate salt or thiourea works to stimulate initiation of flowering shoots when administered at the proper time (Núñez-Eliséa, 1988; Tongumpai et al., 1997). Calcium or potassium nitrate should be spray applied to the undersides of leaves throughout the tree canopy without adjuvant as a 4% (w/v) solution whereas ammonium nitrate should be applied at 2% (w/v). If ready to respond, the entire tree will initiate growth immediately with new shoots visible by 10 d. If tree stems are not sufficiently mature to respond, they usually remain in rest. Repeat biweekly sprays and observations on several test trees are recommended until the desired flowering response is observed, after which the rest of the orchard can be treated with confidence that a flowering response will ensue. This will reduce the cost of repeat sprays to the entire orchard. If a vegetative response is observed on the first application date, it means the stems are too young, likely due to a later or second flush of growth than anticipated following the pruning event (Davenport, 2006). If a vegetative response occurred, then one is advised to wait two months before applying nitrate to a new set of such test trees. Cool night temperatures occurring just before or during the scheduled spray time may result in earlier stimulation of flowering. Once a flowering response is observed, then each section of the orchard, according to the order and timing of pruning, can be sprayed.

In the absence of cool temperatures, the ability to flower is directly correlated with the age of the terminal intercalary unit in tropical climates (Davenport, 2000; F. Ramirez and T.L. Davenport, submitted for publication). The more mature the last flush becomes the more likely it is to produce flowering shoots when stimulated to grow; hence initiation of shoots on young terminal stems is virtually always vegetative in the absence of cool temperatures. If early shoots are initiated and become the new terminal intercalary unit, they reset the perceived age of available stems and delay a possible flowering response beyond the desired time. Management of leaf nitrogen levels is the key to controlling unwanted flushes of vegetative growth especially during the rainy season (Davenport 2003, 2006).

High nitrogen levels, especially under well-watered conditions, are conducive to initiation of frequent vegetative flushes. Reduction of vegetative flushes can be accomplished by limiting nitrogen fertilizer application to trees until the desired flowering time. It is critical to maintain annual leaf nitrogen levels sufficiently low to discourage unwanted flushes of vegetative growth in the months approaching the desired flowering date. The amount of granular nitrogen necessary at flowering for good fruit set and development while preventing unwanted vegetative flushes later should be applied to root zones near the desired flowering time.

Results correlating high leaf nitrogen levels with frequent vegetative flushes in lychee (Menzel et al., 1988, 1992) are directly applicable to management of mango (Davenport, 2003, 2006). It is advisable that leaf analyses should be conducted on the last flush of leaves at least one or, preferably, two times per year. If one analysis is conducted per year, it should be done just prior to the synchronizing prune. The leaf nitrogen levels for mango should be 1.1 to 1.4% at the time of the synchronizing prune event in order to avoid possible second flushes (T.L. Davenport, unpublished observation). The second analysis should be conducted just prior to floral stimulation. Sufficient nitrogen should be applied in the bulk fertilizer at the time of flowering to provide the levels needed to maintain good fruit set and development without retaining any residual nitrogen after harvest that may raise the leaf nitrogen levels for the next synchronizing prune. It is essential that the trees receive all of the other essential macro- and micronutrients for healthy growth. Appropriate levels of P, K, Mg, S, and minor elements are necessary along with a proper balance of calcium and the other cations, as determined by leaf analyses, while managing nitrogen in the low range in order to control the frequency of vegetative flushes.

The type of irrigation used for mangoes, is an important consideration if flowering management is desired. Most growers in the tropics who have irrigation to furnish water to trees through the typical six-month annual dry season use furrow irrigation along the tree rows (personal observation). In-row furrow irrigation has the disadvantage of providing water periodically around the base of trees. The major problem is that many roots outside the limits of the irrigation ditches never get watered during the dry season; hence, water moves from roots located in or near the irrigation ditches to not only the canopy but also out to the dry roots in response to

water potential gradients in the root system (Boyer, 1985; Canny, 1995; Passioura, 1988). This backwards xylem flow towards root tips prevents upward xylem movement of shoot initiating hormones (cytokinins) that are synthesized in root tips (Skene, 1975; Mok, 1994). Cytokinins, instead, accumulate in the tips of the roots. Active water uptake by these roots when the first rains arrive move the accumulated cytokinins to stem buds in the canopy, thus providing the stimulus (Figure 1) to initiate an undesired flush of vegetative growth in insufficiently mature stems when the first rains of the rainy season arrive (Davenport, 2008). In some areas, the first rains of the rainy season stimulate flowering in those stems that have reached sufficient time in rest due to lack of flushes during the dry season.

Drip irrigation provides a constant source of water to the canopy, but it has the same disadvantage of watering only those roots that are located near emitters as does in-row furrow irrigation. Experience has shown that if a grower needs to synchronize prune the orchard during the dry season and water availability becomes limited, then the post-prune flush will not occur until arrival of the first rains (personal observations). If in-row furrow or drip irrigation is available and a post-pruning flush occurs immediately after the prune, then a second flush may occur upon arrival of the first rains, especially if leaf nitrogen levels are greater than 1.4%.

Microjet irrigation has the advantage of providing continuous water availability, but since water is distributed in an area up to 6 m in diameter to most of the roots, the entire root system remains well hydrated throughout the dry period. This discourages the flush that normally occurs after the first rain ending the dry season. Leaf nitrogen levels must be in the range specified above in order to discourage vegetative flushes that tend to occur during the rainy season, especially if that period is between the synchronizing prune event and the nitrate spray dates.

CONCLUSION

Induction of flowering in the subtropics is primarily governed by chilling temperatures from passing cold fronts during winter-spring months. The age of the previous flush modifies the cool-temperature-induced floral response, with older stems exhibiting a higher probability of a floral response and younger stems displaying a higher probability of a vegetative response. In the tropics, however, the age of the last flush is the dominant factor regulating flowering. Stems must be in rest for sufficient time, generally about four to five months to be induced to flower in the absence of chilling temperatures. This extended rest period occurs naturally as trees increase in stature, but it can also be achieved by mild plant water stress or low nitrogen fertility. Moderately cool temperatures that often reach deep into tropical dry and high elevation locations provide additional stimulus to flower in stems of a given age.

Armed with the basic information provided here, growers can manage flowering to occur at any desired week of the year. Local environmental conditions may alter the expected responses, but scrutiny of all of the factors should bring consistent success.

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