

Processes Influencing Floral Initiation and Bloom: The Role of Phytohormones in a Conceptual Flowering Model

Thomas L. Davenport

ADDITIONAL INDEX WORDS. reproductive physiology, temperate fruit, apple, tropical fruit, citrus, mango, lychee, floral induction

SUMMARY. The reproductive phenologies of temperate fruit tree species are briefly introduced and compared to the reproductive phenologies of three tropical and subtropical fruit tree species. The impact of leaf and fruit development and the phytohormones they may produce on the reproductive or vegetative fate of bourse buds in apple spurs serves as the model to discuss temperate fruit flowering. In contrast, conceptual models of citrus (*Citrus* L.), mango (*Mangifera indica* L.), and lychee (*Litchi chinensis* Sonn.) flowering are described which propose physiological mechanisms for both flowering and vegetative flushing in trees grown in subtropical and tropical environments. Possible roles for auxin and cytokinins in shoot initiation and for gibberellins and a putative florigenic promoter in induction are discussed as they relate to the physiology of flowering and vegetative flushing of tropical species. Successful application of these conceptual flowering models through the use of growth regulators and other horticultural management techniques to control flowering of citrus, mango, and lychee is described.

Flowering is the single most important event in the survival of angiosperms. Woody tree species in this phylum have adapted a variety of mechanisms to ensure the success of this event. Fruit-bearing, arboreal species have been selected for cultivation primarily because of their palatable fruit characteristics and qualities that make them particularly attractive. They can be broadly categorized into two main groups, deciduous fruit tree species that grow in temperate climates and evergreen species that thrive in both tropical and subtropical climates. These two groups display phenologies that incorporate adaptations to each climate, including timing of flowering to avoid injurious conditions such as freezing winter temperatures in temperate regions and the desiccating conditions present during dry seasons in the tropics and subtropics.

University of Florida, Tropical Research and Education Center, 18905 SW 280 Street, Homestead, FL 33031; tldav@gnv.ifas.ufl.edu.

Florida Agricultural Experiment Stations journal series R-07187. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be marked *advertisement* solely to indicate this fact.

It is important to note the salient features and differences between the phenologies of these two groups. Because the continental United States is mostly located across a range of temperate latitudes, the majority of horticulturists reading this article are already familiar with temperate fruit phenologies. Less space will, therefore, be devoted to this topic. Areas of Hawaii, southern California, Arizona, Texas, and Florida, however, are major production sites for fruit adapted to the tropics and/or subtropics. My familiarity with the phenologies and possible mechanisms of flowering of tropical and subtropical fruit makes me better able to discuss them in more detail.

DECIDUOUS FRUIT TREE REPRODUCTIVE PHENOLOGY IN TEMPERATE CLIMATES. Because growing seasons last no more than 6 to 8 months in temperate zones, and the time necessary from floral initiation to fruit maturity may last up to 1 year in these conditions, temperate fruit trees have adapted mechanisms to protect the reproductive and vegetative organs through cold winter periods. In general, floral buds initiate in mid to late summer, forming floral structures before the trees become dormant in preparation for winter. Pome fruit, such as apples (*Malus pumila* Mill.) and pears (*Pyrus communis* L.), initiate flowers predominantly in terminal buds of shoots and spurs. Stone fruit, such as plums (*Prunus domestica* L.), peaches (*Prunus persica* L.) and apricots (*Prunus armeniaca* L.), initiate flowers in lateral buds on current season shoots as well as older lateral spurs. A summary of flowering architectures and phenologies of these and other temperate tree crops can be found in Sedgley (1990) and Westwood (1993).

Perhaps the most extensive documented information on temperate tree fruit reproductive physiology can be found for apple (Greene, 1996). Anthesis of temperate tree flowers occurs in early spring. The majority of flowering and fruiting typically occurs in spurs of apple, but some cultivars produce a high percentage of flowers and fruit on longer terminal shoots or in lateral buds. The flowering cycle in spurs begins soon after the break of dormancy in spring before anthesis of floral buds that had formed the previous year. Development is initiated in the bourse bud located in the apex of

vegetative spurs. This bud slowly initiates a series of nodes through the growing season starting with bud scales (typically 7 to 11 in number) followed by two to three transition leaves, three to six true leaves, and finally three bracts (McLaughlin and Greene, 1991). The number of each of these lateral organs varies with cultivar but is relatively constant in each regardless of rootstock (Hirst and Ferree, 1995). Floral induction in the developing bourse bud typically coincides with the transition from true leaf to bract formation, which occurs during the initial period of vegetative growth of the previous year's bourse bud. Numerous factors, however, affect floral induction during this transition and can determine whether it is to remain vegetative or to become reproductive (Dennis, 1967; Greene, 1996).

The presence of small, developing fruit during the transition period is the dominant factor affecting the outcome of the bourse bud. If flowers, initiated during the previous season, set fruit on the spur during the current spring growth, then the bourse bud will, in most cultivars, remain vegetative the following year, giving rise to the strong alternate bearing tendency typical of individual spurs. If, however, no fruit are present on the spur, then floral induction usually occurs; and the floral buds begin differentiation forming individual floral structures before entering winter dormancy. Anthesis occurs during the following spring following a suitable number of winter chilling hours to break bud dormancy (Greene, 1996).

A putative florigenic component appears to be translocated from current season spur leaves to promote flowering in bourse buds. Spur leaf removal (Ramirez and Hoad, 1981), small leaf areas (Huet, 1972), and shading (Cain, 1971) all negatively impact floral induction in bourse buds. Cytokinins, which are present in substantial quantities in spur leaves (Greene, 1975), may participate as this florigenic component since exogenously applied cytokinins can replace the requirement for leaves in the formation of floral buds (Ramirez and Hoad, 1981).

A potent floral inhibitor appears to be produced and transported from seeds of developing fruit to cause bourse buds to remain vegetative (Chan and Cain, 1967). This inhibitor appears to

be GA₇ or closely associated with it (Tromp, 1992). The ratio of these two components, i.e. cytokinins derived from leaves and gibberellins derived from developing fruit, may interact to determine the fate of bourse buds. This point is supported by observations that spurs bearing more than six leaves can overcome the inhibitory effects of the fruit on floral development in bourse buds (Huet, 1972), and the inhibitory impact of gibberellins can be overcome by the cytokinin, benzyladenine (McLaughlin and Greene, 1984).

Because of the alternate bearing tendency of individual spurs, whole trees, or orchards; de-synchronization of the on/off cycle of spurs on trees has been a major goal of horticulturists of temperate tree fruit. Chemical thinning of fruit in on-years or application of gibberellin-synthesis inhibitors early enough to negate the impact of gibberellins on the developing bud are possible key elements in this strategy.

TROPICAL AND SUBTROPICAL FRUIT TREE REPRODUCTIVE PHENOLOGY. Citrus, mango, and lychee are species adapted to tropical and subtropical climates. The growth and development phenologies of these fruit trees differ substantially from those of temperate fruit trees. Tree phenologies and proposed mechanisms of flowering have been reviewed in detail for citrus (Davenport, 1990), mango (Davenport and Nuñez-Elisea, 1997), and lychee (Menzel, 1983, 1984). The flowering phenologies of each of these species are remarkably similar despite the vastly different morphologies. These species thrive and reproduce in tropical as well as in subtropical climates, and their tolerance to freezing temperatures defines the limits of subtropical adaptability in higher latitudes. The focus of published information on flowering of these three species has varied, but the similarities in responses to environmental cues suggest that many of the findings of one species may be applicable to the others.

Individual stems of these three species of tropical fruit trees are dormant most of the time. Growth occurs as periodic, ephemeral flushes of shoots emerging from apical or lateral resting buds before returning to a quiescent state. Stems here are defined as branch tips that are in rest, whereas shoots refer to actively growing branch tips or laterals regardless of type of growth,

shoots are rich sources of auxins and gibberellins, which may be involved in regulating the timing of subsequent shoot initiation. Auxins are actively transported basipetally to roots from production sites in developing shoots (Cane and Wilkins, 1970; Goldsmith, 1968), and they are known to stimulate adventitious root growth in mango and other crops (Hassig, 1974; Nuñez-Elisea et al., 1992). Elevated levels of auxin synthesis in periodically flushing shoots are likely to form a periodic pulse of concentrated auxin, which moves basipetally to the roots. This putative pulse of elevated auxin arriving at the roots may stimulate initiation of new root flushes following each vegetative flush. Alternation of root and shoot growth has been observed in citrus (Bevington and Castle, 1986) and mango (Cull, 1991; T.L. Davenport, unpublished results).

New roots that develop following growth stimulation are known to be a primary source of cytokinins (Itai et al., 1973). Cytokinins are passively transported to shoots via the xylem sap. They have been demonstrated to accumulate in resting stem buds and correlate with shoot initiation of citrus (Hendry et al., 1982; Saidha et al., 1983). Exogenously applied cytokinins stimulate shoot initiation of citrus (Nauer and Boswell, 1981) and mango (Chen, 1985; Nuñez-Elisea et al., 1990). It is well established, however, that auxin inhibits shoot initiation and enforces apical dominance by preventing axillary buds from initiating growth (Davies, 1995). Based on research in other species, it is likely that leaf auxin production and petiolar auxin transport capacity declines as leaves age during stem dormancy (Davenport et al., 1980; Veen and Jacobs, 1969). These observations suggest that auxins (inhibitory) and cytokinins (promotive) may be interactively involved in periodic bud break (Fig. 2). Shoot initiation may be regulated by a critical balance of these two and possibly a third phytohormone (gibberellin A_3 acting indirectly) rather than the absolute concentration of any one of these compounds (Cline, 1997; Cline et al., 1997). During dormant periods, the supply of auxin from leaves to buds of mango decreases with age (Chen, 1987). In contrast, cytokinin levels in buds have been reported to increase over time (Chen, 1987). Perhaps at some point, when a critical cytokinin/

auxin ratio is reached, the bud is initiated, thus, resetting the initiation cycle.

Fruit are rich sources of auxin and gibberellins, which may contribute to the strong inhibition of bud break commonly observed on fruit-bearing stems. The longer fruit remain attached, the longer the post-harvest inhibition of shoot initiation on that stem may last (Davenport, 1990; Kulkarni, 1991; Kulkarni and Rameshwar, 1989).

Foliar-applied nitrogen can also impact shoot initiation. For example, urea enhances initiation of citrus flowering (Ali and Lovatt, 1994; Davenport, 1990). Moreover, foliar-applied potassium, ammonium, or calcium nitrate stimulates shoot initiation of mango in the low-latitude tropics and is widely used there to stimulate flowering (Bondad and Linsangan, 1979; Nuñez-Elisea, 1985; Nuñez-Elisea and Caldeira, 1988). To be successful in stimulating flowering, however, the nitrate salt must be applied after the resting stems of mango have reached sufficient age to overcome any inhibitory influence they may have on the flowering response.

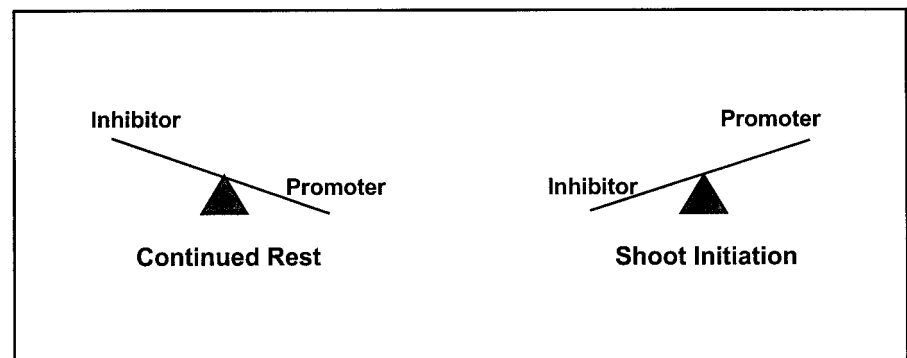
Water stress replaces chilling as the primary trigger for citrus floral induction in areas of the tropics where temperatures are always moderate but which have distinct rainy and dry seasons (Cassin et al., 1969; Reuther and Rios-Castaño, 1969). The direct impact of water stress on flowering of citrus has been covered in detail elsewhere (Davenport, 1990). Whereas water stress has been thought to induce flowering of mango and lychee, there is no conclusive evidence that water stress is directly involved in inductive processes as has been found in citrus (Menzel, 1983; Nuñez-Elisea and Davenport, 1994). Moderately low water potentials delay shoot initiation through reduced turgor, thus

contributing to extending the age of stems and reducing the levels of a putative floral inhibitor (vegetative promoter) that is proposed to reside in the leaves (Kulkarni, 1991; Nuñez-Elisea and Davenport, 1994).

Exogenously applied gibberellic acid (GA_3) inhibits flowering of both citrus (Davenport, 1990; Guardiola et al., 1982) and mango (Nuñez-Elisea and Davenport, 1991b). It is yet not clear whether this phytohormone impacts floral induction in citrus or whether it only impacts shoot initiation as seems to be the case for mango (Nuñez-Elisea and Davenport, 1998; Tomer, 1984). The normal presence of this phytohormone in leaves, buds, and fruit of mango (Chen, 1987; Davenport et al., 2000) suggests that GA_3 may interact with auxin to inhibit shoot initiation. GA_3 was not detected in citrus leaves (Poling and Maier, 1988), which suggests that it may be metabolized to another compound to influence its impact on flowering when exogenously applied. Observations of early flowering in mango trees treated with paclobutrazol is likely a response to lowered GA_3 levels, thus lowering the overall level of inhibition of shoot initiation (Davenport and Nuñez-Elisea, 1990; Voon et al., 1991).

Evidence indicates that the induction switch is governed in all of these tropical species by the interaction of a putative floral promoter, which is up-regulated during exposure to

Fig. 2. Possible interaction of phytohormones regulating shoot initiation. 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.



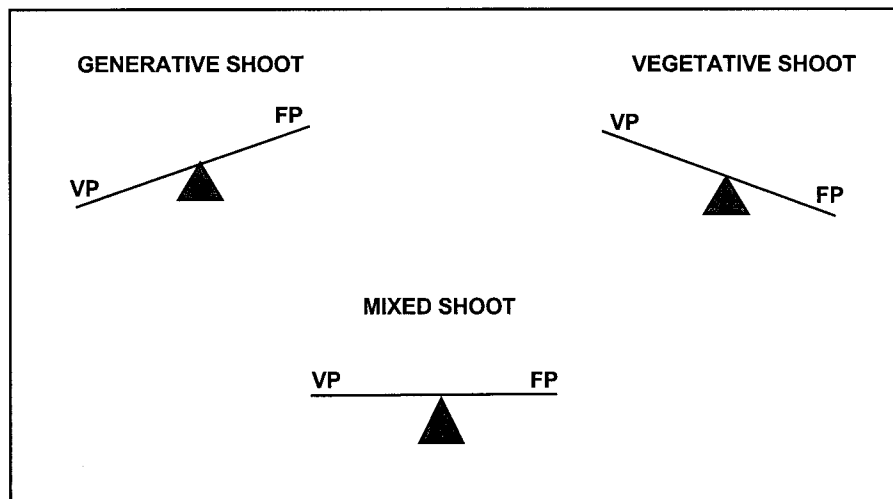


Fig. 3. Possible interaction of phytohormones regulating shoot induction. The ratio of a putative floral promoter (FP) and a vegetative promoter (VP, possibly a gibberellin) may direct the type of shoot that is displayed at the time of initiation. A low ratio of floral to vegetative promoter is conducive 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.

low-temperature, with an age-regulated vegetative promoter, possibly a gibberellin other than GA_3 , in leaves or buds at the time of shoot initiation. The floral promoter appears to be located in the stem tips of citrus and in leaves of mango. In mango, it is transported to buds probably via phloem (Davenport and Nuñez-Elisea, 1990; Nuñez-Elisea and Davenport, 1989, 1992; Nuñez-Elisea et al., 1996) and is graft transmissible (Kulkarni, 1986, 1988, 1991). Attempts to identify the putative floral promoter, however, have been unsuccessful. The vegetative promoter may be a gibberellin since triazoles and other classes of plant growth retardants, which inhibit gibberellin biosynthesis, promote strong and out-of-season flowering in younger stems under conditions that would normally be marginally or noninductive (Nuñez-Elisea et al., 1993). High floral/vegetative promoter ratios when initiation occurs may, thus, be conducive to induction of generative shoots (Fig. 3). Low ratios may be conducive to induction of vegetative shoots, and an intermediate ratio of the two may be conducive to induction of mixed shoots. Regardless of the endogenous

levels of the individual components perceived in buds at the time of initiation, flowering and vegetative growth responses can be effectively explained by the ratio of the floral and vegetative promoters.

Although the putative floral promoter seems to be up-regulated during exposure to cool night temperatures [below 18 °C (64 °F)], there appears to be a base level present at all times regardless of temperature. Flowering of mango occurs in tropical areas that lack cool night temperatures only when shoots become sufficiently aged (Nuñez-Elisea and Davenport, 1995). It is plausible that the ratio of the base level of putative resident floral promoter and vegetative promoter increases to a critical threshold over time due to decreased vegetative promoter levels, resulting in floral induction when shoots are initiated. This may explain how flowering occurs on some branches throughout the year in citrus and mangoes growing in low-latitude tropics. High proportions of mixed shoots are commonly found in these conditions, indicating marginally floral inductive ratios. In contrast, flowering in young stems, conceivably having higher levels of vegetative promoter, is observed only when initiation occurs during exposure to cool, floral-inductive temperatures (Davenport, 1990; Menzel, 1983; Nuñez-Elisea and Davenport, 1995). The flowering response to chilling temperatures in these stems could, therefore, be attributed to the higher ratio between the up-regulated floral promoter and the resident vegetative promoter.

Photoassimilates produced by leaves provide carbohydrates essential for development of roots and other

vital plant organs, including fruit, when present. Further experimental results are needed to clarify the role of carbohydrates in shoot initiation or induction.

This model is consistent with growth and development patterns taking place in citrus, mango, and lychee trees growing in both the tropics and subtropics throughout the world. It, however, remains conceptual, especially with regard to the regulatory details. Current and future research efforts will continue to revise and refine the model by testing the validity of the hypotheses embedded in it. It is hoped that a realistic understanding of the mechanisms of flowering and vegetative growth in tropical fruit trees will result.

Citrus, mango and lychee growers have been able to improve production and manipulate the timing of their crops through the application of concepts summarized here. Citrus growers in the subtropics are realizing a greater amount of flowering and yield after application of urea (Ali and Lovatt, 1994), and those in the tropics use water stress to stimulate flowering when desired (Cassin et al., 1969). Mango growers can now stimulate flowering and subsequent cropping at any time of the year in the Northern or Southern Hemisphere tropics. They do this using mild water stress or low nitrogen fertilization to reduce leaf nitrogen levels and discourage flushes for at least 6 months before stimulation of a flowering flush using foliar nitrate spray. More commonly, growers now apply paclobutrazol to substitute for the age requirement provided by mild water stress or low nitrogen to obtain flowering on younger stems (Kulkarni and Hamilton, 1996; Nartvaranant et al., 1999). Lychee growers are achieving more reliable flowering, especially in low-production cultivars by discouraging fall vegetative flushes, thus insuring adequate age of the stems when the cool night temperatures occur in winter (Menzel, 1983).

In conclusion, both the temperate and tropical and subtropical fruit tree species demonstrate flowering phenologies that are well adapted to the environments in which they originated. Specific roles for phytohormones have been implicated in both groups to explain the mechanisms of flowering and timing of the event. Both groups appear to utilize a flower-

ing promoter, which in some cases in both groups has been demonstrated to be produced in leaves and translocated to buds. Cytokinins have been associated with floral induction in deciduous fruit crops whereas this class of phytohormone has been implicated in shoot initiation in resting buds of tropical species. Components (perhaps $GA_{4/7}$) translocated from seeds of apple appear to function as a vegetative promoter. Although $GA_{4/7}$ is not present in mango, GA_3 from seeds and leaves may interact with auxin to participate in inhibition of shoot initiation (Davenport et al., 2000), and an unidentified gibberellin in leaves may act as the vegetative promoter (Davenport and Nuñez-Elisea, 1997). The ratio of the putative floral and vegetative promoters appears to regulate the reproductive or vegetative fate of both the bourse buds in temperate fruit trees and the buds of tropical plants as they initiate growth.

It is plausible to consider that the floral promoter in apple is dependant upon cool temperatures of spring to enable floral induction at the appropriate time, as is the case of tropical plants. If this were the case, then the similarity of roles for the various classes of phytohormones warrants further comparisons between these two diverse groups of plants. Future research may be able to resolve this point.

Literature cited

- Ali, A.G. and C.J. Lovatt. 1994. Winter application of low-biuret urea to the foliage of 'Washington' navel orange increased yield. *J. Amer. Soc. Hort. Sci.* 119:1144-1150.
- Batten, D.J. and C.A. McConchie. 1995. Floral induction in growing buds of lychee (*Litchi chinensis*) and mango (*Mangifera indica*). *Austral. J. Plant Physiol.* 22:783-791.
- Bernier, G. 1988. The control of floral evocation and morphogenesis. *Annu. Rev. Plant Physiol.* 39:175-219.
- Bernier, G., A. Havelange, C. Houssa, A. Petitjean, and P. Lejeune. 1993. Physiological signals that induce flowering. *Plant Cell* 5:1147-1155.
- Bevington, K.B. and W.S. Castle. 1986. Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature, and soil water content. *J. Amer. Soc. Hort. Sci.* 110:840-845.
- Bondad, N.D. and E. Linsangan. 1979. Flowering in mango induced with potassium nitrate. *HortScience* 14:527-528.
- Cain, J.C. 1971. Effect of mechanical pruning of apple hedgerows with a slotted saw on light penetration and fruiting. *J. Amer. Soc. Hort. Sci.* 96:664-667.
- Cane, A.R. and M.B. Wilkins. 1970. Auxin transport in roots. *J. Expt. Bot.* 21:212-218.
- Cassin, J., B. Bourdeaut, F. Fougue, V. Furin, J.P. Gaillard, J. Le Bourdelles, C. Montigut, and C. Monevil. 1969. The influence of climate upon the blooming of citrus in tropical areas. *Proc. 1st Intl. Citrus Symp.* 1:315-323.
- Chan, B.G. and J.C. Cain. 1967. The effects of seed formation in subsequent flowering in apple. *Proc. Amer. Soc. Hort. Sci.* 91:63-68.
- Chen, W.S. 1985. Flower induction in mango (*Mangifera indica* L.) with plant growth substances. *Proc. Natl. Sci. Council Part B, Life Sci. Taipei, Rep. China* 9:9-12.
- Chen, W.S. 1987. Endogenous growth substances in relation to shoot growth and flower bud development of mango. *J. Amer. Soc. Hort. Sci.* 112:360-363.
- Cline, M.G. 1997. Concepts and terminology of apical dominance. *Amer. J. Bot.* 84:1064-1069.
- Cline, M.G., T. Wessel, and H. Iwamura. 1997. Cytokinin/auxin control of apical dominance in *Ipomoea nil*. *Plant Cell Physiol.* 38:659-667.
- Cull, B.W. 1991. Mango crop management. *Acta Hort.* 291:154-173.
- Davenport, T.L. 1986. Avocado flowering. *Hort. Rev.* 8:257-289.
- Davenport, T.L. 1990. Citrus flowering. *Hort. Rev.* 12:349-408.
- Davenport, T.L., P.W. Morgan, and W.R. Jordan. 1980. Reduction of auxin transport capacity with age and internal water deficits in cotton petioles. *Plant Physiol.* 65:1023-1025.
- Davenport, T.L. and R. Nuñez-Elisea. 1990. Ethylene and other endogenous factors possibly involved in mango flowering. *Acta Hort.* 275:441-448.
- Davenport, T.L. and R. Nuñez-Elisea. 1997. Reproductive physiology, p. 69-146. In: R.E. Litz (ed.). *Mango botany, production and use*. CAB Intl., Wallingford Oxon, U.K.
- Davenport, T.L., Pearce, D.W., Rood, S.B. 2000. Correlation of endogenous gibberellic acid with initiation of mango shoot growth. *J. Plant Growth Reg.* (in press).
- Davies, P.J. (ed.). 1995. *Plant hormones—Physiology, biochemistry and molecular biology*. Kluwer, Boston.
- Dennis, F.G. 1967. The physiology of flowering and fruit set in fruit trees. *Proc. Ore. Hort. Soc.* 77:33-43.
- Goldsmith, M.H.M. 1968. The transport of auxin. *Annu. Rev. Plant Physiol.* 19:347-360.
- Greene, D.W. 1975. Cytokinin activity in the xylem sap and extracts of MM 106 apple rootstocks. *HortScience* 10:73-74.
- Greene, D.W. 1996. Flower development, p. 91-98. In: M. Marl, P. Andrew, G. Lang, and K. Mullinex (eds.). *Tree fruit physiology: Growth and development*. Good Fruit Grower, Yakima, Wash.
- Guardiola, J.L., C. Monerri, and M. Agusti. 1982. The inhibitory effect of gibberellic acid on flowering in Citrus. *Physiol. Plant.* 55:136-142.
- Hassig, B.E. 1974. Origins of adventitious roots. *N.Z. J. For. Sci.* 4:229-310.
- Hendry, N.S., J. van Staden, and P. Allan, 1982. Cytokinins in citrus. II. Fluctuations during growth in juvenile and adult plants. *Scientia Hort.* 17:247-256.
- Hirst, P.M. and D.C. Ferree, 1995. Rootstock effects on 'Delicious' apple. I. Bud development. *J. Amer. Soc. Hort. Sci.* 120:1010-1017.
- Huet, J. 1972. Etude des effets leveles et des fruits sur l'induction florale brachyblastes du poirier. *Physiol. Vegetale* 10:529-545.
- Itai, C., A. Ben-Zioni, and L. Ordin. 1973. Correlative changes in endogenous hormone levels and shoot growth induced by short heat treatments to the root. *Physiol. Plant.* 29:355-360.
- Kinet, J.M. 1993. Environmental, chemical, and genetic control of flowering. *Hort. Rev.* 15:279-334.
- Kulkarni, V.J. 1986. Graft-induced off-season flowering and fruiting in the mango (*Mangifera indica* L.). *J. Hort. Sci.* 61:141-145.
- Kulkarni, V.J. 1988. Further studies on graft-induced off-season flowering and fruiting in mango (*Mangifera indica* L.). *J. Hort. Sci.* 63:361-367.
- Kulkarni, V.J. 1991. Physiology of flowering in mango studied by grafting. *Acta Hort.* 291:95-104.
- Kulkarni, V. and D. Hamilton. 1996. An integrated approach towards improving mango productivity. *Acta Hort.* 455:84-91.
- Kulkarni, V.J. and A. Rameshwar. 1989. Effect of deblossoming and defruiting on off-season flowering and fruiting in mango (*Mangifera indica* L.). *Scientia Hort.* 39:143-148.
- McLaughlin, J.M. and D.W. Greene. 1984. Effect of BA, $GA_{4/7}$ and daminozide on fruit set, fruit quality, vegetative growth, flower initiation, and flower quality in Golden Delicious apple. *J. Amer. Soc. Hort. Sci.* 109:34-39.
- McLaughlin, J.M. and D.W. Greene. 1991. Fruit and hormones influence flowering of apple. I. Effect of cultivar. *J. Amer. Soc. Hort. Sci.* 116:446-449.
- Menzel, C.M. 1983. The control of floral initiation in lychee: a review. *Scientia Hort.* 21:201-215.
- Menzel, C.M. 1984. The pattern and control of

- reproductive development in lychee: a review. *Scientia Hort.* 22:333-345.
- Nartvaranant, P., S. Subhadrabandhu, and P. Tongumpai. 1999. Practical aspect in producing off-season mango in Thailand. *Acta Hort.* (in press).
- Nauer, E.M. and S.B. Boswell. 1981. Stimulating growth of quiescent citrus buds with 6-benzylamino purine. *HortScience* 16:162-163.
- Nuñez-Elisea, R. 1985. Flowering and fruit set of a monoembryonic and polyembryonic mango as influenced by potassium nitrate sprays and shoot decapitation. *Proc. Fla. State Hort. Soc.* 98:179-183.
- Nuñez-Elisea, R. and M.L. Caldeira. 1988. Induction of flowering in mango (*Mangifera indica*) with ammonium nitrate sprays. *HortScience* 23:833.
- Nuñez-Elisea, R., M.L. Caldeira, and T.L. Davenport. 1990. Thidiazuron effects on growth initiation and expression in mango (*Mangifera indica* L.). *HortScience* 25:1167 (abstr.).
- Nuñez-Elisea, R., M.L. Caldeira, W. Ferreira, and T.L. Davenport. 1992. Adventitious rooting of 'Tommy Atkins' mango air layers induced with naphthaleneacetic acid. *HortScience* 27:926.
- Nuñez-Elisea, R. and T.L. Davenport. 1989. Expression of an endogenous flowering promoter in mango (*Mangifera indica*). *Proc. 16th Annu. Meet. Plant Growth Reg. Soc. Amer.* p. 245-247.
- Nuñez-Elisea, R. and T.L. Davenport. 1991a. Effect of duration of low temperature treatment on flowering of containerized 'Tommy Atkins' mango. *Proc. 18th Annu. Meet. Plant Growth Reg. Soc. Amer.* p. 39-41.
- Nuñez-Elisea, R. and T.L. Davenport. 1991b. Flowering of 'Keitt' mango in response to deblossoming and gibberellic acid. *Proc. Fla. State Hort. Soc.* 104:41-43.
- Nuñez-Elisea, R. and T.L. Davenport. 1992. Requirement for mature leaves during floral induction and floral transition in developing shoots of mango. *Acta Hort.* 296: 33-37.
- Nuñez-Elisea, R. and T.L. Davenport. 1994. Flowering of mango trees in containers as influenced by seasonal temperature and water stress. *Scientia Hort.* 58:57-66.
- Nuñez-Elisea, R. and T.L. Davenport. 1995. Effect of leaf age, duration of cool temperature treatment, and photoperiod on bud dormancy release and floral initiation in mango. *Scientia Hort.* 62:63-73.
- Nuñez-Elisea, R. and T.L. Davenport. 1998. Gibberellin and temperature effects on dormancy release and shoot morphogenesis of mango (*Mangifera indica* L.). *Scientia Hort.* 77:11-21.
- Nuñez-Elisea, R., T.L. Davenport, and M.L. Caldeira. 1991. An experimental system to study mango flowering using containerized trees propagated by air-layering. *Proc. Fla. State Hort. Soc.* 104:39-41.
- Nuñez-Elisea, R., T.L. Davenport, and M.L. Caldeira. 1993. Bud initiation and morphogenesis in 'Tommy Atkins' mango as affected by temperature and triazole growth retardants. *Acta Hort.* 341:192-198.
- Nuñez-Elisea, R., T.L. Davenport, and M.L. Caldeira. 1996. Control of bud morphogenesis in mango (*Mangifera indica* L.) by girdling, defoliation and temperature modification. *J. Hort. Sci.* 71:25-40.
- Poling, S.M. and V.P. Maier. 1988. Identification of gibberellins in navel oranges. *Plant Physiol.* 88:639-670.
- Ramirez, H. and G.V. Hoad. 1981. Effect of growth substances on fruit-bud initiation in apple. *Acta Hort.* 120:131-136.
- Reuther, W. and D. Rios-Castaño. 1969. Comparison of growth, maturation and composition of citrus fruits in subtropical California and tropical Columbia, p. 277-300. In: H.D. Chapman (ed.). *Proc. 1st Intl. Citrus Symp.* Univ. of Calif., Riverside.
- Saidha, T., E.E. Goldschmidt, and S.P. Monselise. 1983. Endogenous growth regulators in tracheal sap of citrus. *HortScience* 18:231-232.
- Sedgley, M. 1990. Flowering of deciduous perennial fruit crops. *Hort. Rev.* 12:223-264.
- Southwick, S.M. and T.L. Davenport. 1986. Characterization of water stress and low temperature effects on flower induction in citrus. *Plant Physiol.* 81:26-29.
- Southwick, S.M. and T.L. Davenport. 1987. Modification of the water stress-induced floral response in 'Tahiti' lime. *J. Amer. Soc. Hort. Sci.* 112(2):231-236.
- Tomer, E. 1984. Inhibition of flowering in mango by gibberellic acid. *Scientia Hort.* 24:299-303.
- Tromp, J. 1992. Flower bud formation in apple as affected by various gibberellins. *J. Hort. Sci.* 57:277-282.
- Veen, H. and W.P. Jacobs. 1969. Transport and metabolism of indole-3-acetic acid in coleus petiole segments of increasing age. *Plant Physiology* 44:1157-1162.
- Voon, C.H., C. Pitakpaivan, and S.J. Tan. 1991. Mango cropping manipulation with Cultar. *Acta Hort.* 291:219-228.
- Westwood, M.N. 1993. Temperate-zone pomology: Physiology and culture. 3rd ed. Timber Press, Portland.