# *MODERN CONCEPTS OF FLORA DEVELOPMENT AN ITS APPLICATION IN HORTICULTURE INDUSTRY*

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I have immense pleasure in presenting this Report presentation

On Modern concepts of flora development an its application in horticulture industry.
Thank you Dr. Pritam Chattopadhyay sir for give this dissertation topic
.
The subject is an interesting one .It gave me an opportunity to have detailed study on the subject and showed how to thing work in the practical world .
I came to understand and analyze the importance and the role of horticulture industry.
I had a great time working on the report presentation. I have provided information to the fullest of internet ,knowledge and finding one self..

# Modern concept of floral development and its application in horticulture

## INTRODUCTION

Flowers' importance in nature is everywhere they can feed insects, birds, animals and humans; provide natural medicines for humans and some animals; and aid in a plant's reproduction by enticing outside pollinators. Without flowers, plants would merely be green, and the world would be a duller place. The main purpose of flowers is to aid in plant reproduction. Flowers provide an eye-catching attribute to an otherwise plain, green-leaved plant. When insects, birds and some bats dip down to take a look at the flower and steal its nectar, they are inadvertently pollinating the plants by moving pollen or plant sperm from the male stamens to the female pistils. The flower is the most complex structure of plants. Flowers distinguish the most recently diverged plant lineage, the angiosperms or flowering plants, from the other land plants. Flower structure has been studied in a variety of ways. Studies of the natural history and evolutionary biology of flowers have emphasized understanding the ultimate (evolutionary) causes of the wide range of variants such as color, symmetry, meristic arrangements (e.g. flower organ number), size, pollination syndrome, etc. Other studies have addressed the cellular, tissue type, morphological and physical factors that can account for both the phenotypic plasticity and developmental constraints in flower form [Endress P.K. Angiosperm floral evolution: Morphological developmental framework. In: Soltis D.E., Leebens-Mack J.H., Soltis P.S., editors. Advances in botanical research, incorporating advances in plant pathology. Developmental genetics of the flower. 1. Vol. 44. Vol. 8. California: Academic Press; 2006. pp. 2–61]. A different approach flourished in the late 1980s

and early 1990s, the molecular genetics of flower development in two model eudicot species: *Arabidopsis thaliana* and *Antirrhinum majus* [(Plant development going MADS. Jack T, Plant Mol Biol. 2001 Jul; 46(5):515-20), (Molecular mechanisms of flower development: an armchair guide. Krizek BA, Fletcher JC, Nat Rev Genet. 2005 Sep; 6(9):688-98), (Molecular mechanisms underlying origin and diversification of the angiosperm flower. Theissen G, Melzer R. Ann Bot. 2007 Sep; 100(3):603-19)]

Nectar for Insects, Birds and Bats: There are a variety of insects that feast on the nectar of flowers, but the most notable ones are bees, wasps, ants and butterflies. Because these flowers rely on an outward source to pollinate them, some plants have evolved to make themselves even more attractive to their pollinators. The bee orchid has even evolved so that it appears as if a female bee is on the orchid, when in fact the "bee" is actually part of the flower. The hibiscus and trumpet vine flowers have evolved so that their nectar can be easily taken and their pollen easily transmitted by hummingbirds and sunbirds.

Nectar and pollen-eating bats feed on flowers from agave, organ pipe, cardon and saguaro, these plants have evolved to only open their flowers at night, thus releasing their nectar and pollen when it is convenient for bats.

Food Source for Humans: Rose petals have been used in cooking and teas for centuries, as have day lilies, dandelions, carnations, clovers and daisies. Citrus and banana flowers can also be a food source. The blossoms from chives, garlic, basil, jasmine, lavender, oregano and sage can be used as herbs and spices in food dishes. Other flowers, such as mint, chamomile, ginger and Angelica, can be used in teas.

Food Source for Animals: Deer and rabbits are the biggest flower predators in the animal kingdom. Geraniums and pansies are the first to be eaten, as are flowering

vegetables. Raccoons, skunks and groundhogs also nibble on flowers from time to time.

Medicinal Aids: Many flowers have medicinal uses, such as begonia for eliminating toxins in the body, and calendula, sunflower and honeysuckle for treating sore throats and tonsillitis. Cornflower can be used to treat acne, while valerian and California poppy relieve menstrual cramps. Cats even use flowers to cause vomiting and thus eliminate stomach distress.

Flower morphology results from the interaction of an established genetic program, the influence of external forces induced by pollination systems, and physical forces acting before, during and after initiation. Genetic studies of floral homeotic mutants in both plant species yielded the now classic combinatorial ABC developmental model for floral organ determination [(Genes directing flower development in Arabidopsis.Bowman JL, Smyth DR, Meyerowitz EM. Plant Cell. 1989 Jan; 1(1):37-52), (The war of the whorls: genetic interactions controlling flower development. Coen ES, Meyerowitz EM. Nature. 1991 Sep 5; 353(6339):31-7)].

**Flower Development:**

*Arabidopsis* flowers originate as small groups of undifferentiated cells called flower meristems on the flanks of the inflorescence (shoot) meristem. In contrast to the indeterminate shoot meristem which essentially gives rise to flower primordia indefinitely, flowers are determinate structures that produce a defined number of organ primordia. These organ primordia reside in four concentric rings called whorls, with four sepals in the outermost first whorl, followed by four petals, six stamens, and two fused carpels in the 2nd, 3rd, and 4th whorls, respectively.

There are numerous genes required for the initiation and development of flowers,

and for simplicity they can be divided into distinct classes.

The first class are Flowering Time genes, mutations in which cause early or late flowering. Flowering Time genes can themselves be divided into distinct classes, based on their differential responses to a number of environmental conditions, such as day length and vernalization.

The second class specifies Meristem Identity, and includes genes such as LEAFY, APETALA1, and CAULIFLOWER which specify flower meristem identity, as well as TERMINAL FLOWER which maintains inflorescence meristem identity.

A third class includes the Flower Organ Identity genes, which determine the fate of organ primordia and are incorporated into the "ABC" model of flower development. Examples of organ identity genes include APETALA1 (which is involved in both meristem and organ identity), APETALA2, APETALA 3, PISTILLATA and AGAMOUS.

A fourth class includes late-acting genes that control ovule development and extensive genetic and recent molecular studies have begun to uncover the complex array of interactions among genes in this class. These scientists identified homeotic mutations that resulted in the misplacement of floral organs.

Three classes of mutations were identified in Arabidopsis.

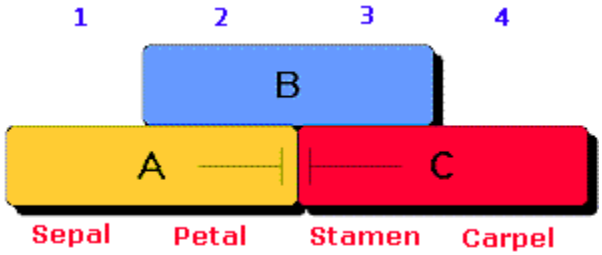
Class A: flowers with these mutations have (unfused) carpels instead of sepals in whorl 1, and stamens instead of petals in whorl 2. The pattern of organs (from outside to inside) is carpel, stamen, stamen, carpel. The genes containing these mutations were named APETALA1 (AP1) and APETALA2 (ap2). Below is an image of an apetala2 mutant flower (right) next to a wild type flower (left).

Class B: flowers with these mutations have sepals in whorl 2 instead of petals, and

(unfused) carpels in whorl 3 instead of stamens. The pattern of organs (from outside to inside) is sepal, sepal,carpel, carpel. The genes containing these mutations were named APETALA3 (AP3) and PISTILLATA (PI). Below is an image of a pistillata mutant flower (right) next to a wild type flower (left).

Class C: flowers with this mutation have petals in whorl 3 instead of stamens, and sepals in whorl 4 instead of carpels. In addition, the floral meristem is not determinate - flowers continue to form within the flowers, so the pattern of organs (from outside to inside) is: sepal, petal, petal; sepal, petal, petal; sepal, petal, petal, etc. The gene containing this mutation was called AGAMOUS (AG). Below is an image of an agamous mutant flower (right) next to a wild type flower (left).

**The ABC model:** Each class of genes is required in two adjacent whorls. Class A genes are required in whorls 1 and 2, class B genes are required in whorls 2 and 3, and class C genes are required in whorls 3 and 4. Both class A and class B genes are required in whorl 2, and both class B and class C genes are required in whorl 3. The ABC model that summarizes these results is shown below. We'll talk in class about how this model has been tested.




**Molecular basis of differentiation:**

The A, B, and C genes are transcription factors. Different transcription factors are

needed together to turn on a developmental gene program such as A and B needed to initiate the program for petals.

Horticulture is a segment of the agriculture industry. The term horticulture literally means the culture of a garden. However, the term has taken on a broader context. Horticulture includes the production and use of plants for food, comfort, and beautification. A direct relationship exists between horticulture and science. The area of science most closely associated with horticulture is botany. Botany is the study of plants and plant processes. The field of science that deals with the cultivation of horticultural plants is known as horticulture science.

Science is applied across the horticulture industry. The application of science to horticulture is called horticulture technology. Successfully raising horticultural plants takes more than just daily watering. Time, patience, and an understanding of diverse scientific processes are needed to produce optimal plant growth.

The horticulture industry can be divided into three areas: pomology, olericulture and floriculture.

Pomology: The term is derived from Latin words poma and logus. Poma means ‘fruit’ and logus means ‘study, knowledge or discourse’. It can be defined as a branch of horticulture, which deals with the scientific study of fruit crops.

Olericulture: The term is derived from Latin words olerus meaning ‘vegetables’ and cultura meaning ‘cultivation’. It can be defined as a branch of horticulture, which deals with the scientific study of vegetable crops.

Floriculture: The term floriculture is derived from Latin words florus and cultura. Florus means ‘flower’ and cultura means ‘cultivation’. It can be defined as a branch of horticulture, which deals with the scientific study of flowering and ornamental crops. Landscape horticulture is a broad category that includes plants for the

landscape, including lawn turf but particularly nursery crops such as shrubs, trees, and vines.

## Significance of Horticulture

Horticulture crops perform a vital role in the Indian economy by generating employment, providing raw material to various food processing industries, and higher farm profitability due to higher production and export earnings from foreign exchange.

1. Horticulture crops are a source of variability in farm produce and diets.
2. They are a source of nutrients, vitamins, minerals, flavour, aroma, dietary fibres, etc.
3. They contain health benefiting compounds and medicines.
4. These crops have aesthetic value and protect the environment.
5. The comparative production per unit area of horticultural crops is higher than field crops, e.g., paddy crop gives a maximum yield of only 30 q/ha, while banana crop gives 300–450 q/ha and grapes 90–150 q/ha.
6. Fruit and plantation crops can be cultivated in places where the slope of land is uneven or undulating. Mango and cashew nut are cultivated on a large scale in hilly and hill back area of the Konkan region.
7. The crops are useful for cultivation in wasteland or poor quality soil.
8. Such crops are of high value, labour intensive and generate employment throughout the year.
9. Horticultural produce serves as raw material for various industries, such as processing, pharmaceutical, perfumery and cosmetics, chemical, confectionery, oils and paints, etc.
10. They have national and international demand and are a good source of foreign

exchange.

**Available horticultural crops in India:** According to the data provided by the Government of India for 2016–17, horticulture crops in India are being cultivated in 24 million hectares, which is about 7 per cent of India's total cropped area. The annual horticultural produce is estimated around 295 million tonnes, which includes 175 million tonnes of vegetables and 92 million tonnes of fruits in 2016–17 (Horticulture Statistics at a Glance 2017, National Horticulture Board, Government of India).

India is the largest producer of okra (lady's finger). Among vegetables, India ranks second in the production of potato, onion, cauliflower, brinjal and cabbage. In fruits, it is the largest producer of banana, mango, guava, lemon and papaya. Mango, walnut, grapes, banana and pomegranate are the major fruits exported, while onion, okra, bitter gourd, green chili, mushroom and potato have more exotic demand. Fruits and vegetables are mostly exported to the UAE, Bangladesh, Malaysia, the Netherlands, Sri Lanka, Nepal, the UK and Saudi Arabia.

**Prospects of horticultural crops in India:** Diverse agro-climatic conditions in India ensure the production of all types of fresh fruits, vegetables and medicinal plants in different parts of the country. Health consciousness among people is increasing. Majority of the population in India is vegetarian. As a result, the demand of fruits and vegetables is also high. The production of horticultural commodities is far less as compared to the existing demand in the country. So, there is a vast scope to produce more horticultural crops. Major areas in the country are suitable only for horticultural crops, like mango, tea, coconut and arecanut, as they are non-arable, rocky, stony, marshy, undulated and sloppy. There has been an increase in irrigation facilities but there are crops, which even

with little watering, can survive. One only needs to ensure adequate water management. Some dry land horticultural crops, like jamun, ber, tamarind, wood apple, custard apple, ramphal, etc., can be grown on rainfed land also. Compared to other countries, agricultural labour and other agricultural inputs are far cheaper and easily available here, which reduce the cost of production and generate more profit. High return, coupled with government assistance, through various schemes and financial aid, attract the rich and poor, trained and educated people towards horticulture. This leads to the use of intensive methods and improved technology in the production of horticultural crops. Awareness of storage and processing methods also increase the availability of the produce, job opportunity and income generation.

## DISCUSSION

In the last few decades, this sector has gained prominence over contributing a growing share in Gross Value Addition of the Agriculture and allied sectors. Mission for Integrated Development of Horticulture (MIDH) is being implemented by adopting an end to end approach for increasing production of horticulture crops and reducing post-harvest losses. Indian Council of Agricultural Resource (ICAR), an autonomous organisation under the Department of Agricultural Research and Education (DARE). Formerly known as Imperial Council of Agricultural Research, it was established on 16 July 1929. Headquartered at New Delhi. It is the apex body for coordinating, guiding and managing research and education in agriculture including horticulture, fisheries and animal sciences in the entire country. National Horticulture Board

(NHB), was set up in 1984 on the basis of recommendations of the "Group on Perishable Agricultural Commodities", headed by Dr M. S. Swaminathan. Headquartered at Gurugram. Objective is to improve integrated development of Horticulture industry and to help in coordinating, sustaining the production and processing of fruits and vegetables. The production of fruits and vegetables has overcome the production of food grains in the country. The total horticulture production has increased from 211.2 million tonnes in 2007-08 to 311.71 million tonnes in 2018-19. India is the second largest producer of fruits and vegetables in the world with first rank in the production of Banana, Mango, Lime & Lemon, Papaya and Okra.

Classification of vegetable crops: If the growing of each vegetable is dealt with in detail, it will lead to too much repetition. It is, therefore, desirable to classify vegetable crops into certain groups as per their similarities

**Based on the nature of plant (stem)**

A. Herbaceous and succulents: Leafy vegetables
B. Shrubs: Brinjal, chilli, tomato, etc.
C. Trees: Drumstick, jackfruit, etc.
D. Vines: Cucurbits, etc.

**Based on the life span (from seed-to-seed)**

A. Annuals: The life span of annual plants or annuals is a season or a year, e.g., brinjal, chilli, cabbage, cauliflower, cucurbits, tomato, leafy vegetables, etc.
B. Biennials: The life span of biennials is of two seasons or two years, e.g. onion, radish, carrot, etc.

C. Perennials: The life span of perennial plants is more than two years, e.g., drumstick (moringa), asparagus (shatawari), pointed gourd (parwal), etc.

**Based on the method of commercial propagation**

A. Sexually propagated (by seed): Brinjal, chilli, cauliflower, cabbage, cucurbits, tomato, leafy vegetables, etc.

B. Asexually propagated (vegetative parts): Asparagus, dioscorea, potato, sweet potato, onion, garlic, taro, yam, etc. (Cuttings: Asparagus, Bulbs: Onion, garlic, Rhizomes: Colocasia, ginger, coleus, Tubers: Potato, sweet potato)

**Based on the method of planting**

A. Directly sown plants: Okra, leafy vegetables, carrot, radish, peas and beans

B. Transplanting: Tomato, brinjal, chilli, cauliflower, cabbage, onion, potato, sweet potato, cassava, pointed gourd, etc.

C. Crops grown from underground parts (Root vegetables: Radish, carrot, turnip, beetroot, Rhizome: Colocasia, ginger, Bulb: Onion, garlic, Tuber: Potato, sweet potato, cassava and yam)

**Based on intercultural practices**

A. Solanaceous crops: Tomato, brinjal, chilli, bell pepper, potato

B. (b) Cole crops: Cabbage, cauliflower, knol-khol, broccoli and Brussels sprouts

C. (c) Leafy vegetables: Spinach, methi, lettuce and chaulai (amaranthus)

D. (d) Pods or capsules: Pea, cowpea, cluster bean, okra

E. (e) Cucurbits: Gourds, melons, cucumber, pumpkin

F. (f) Root crops: Carrot, radish, turnip, beetroot

**Based on climatic requirements**

A. Temperate vegetables: Radish, potato, carrot, cabbage, cauliflower, knol-khol, broccoli, etc.

B. (b) Tropical and subtropical vegetables: Watermelon, musk melon, cucumber, tomato, brinjal, chilli, etc.

**Based on the season of growth**

In India, seasonal or annual vegetables can be classified according to their season of growth. Season of growth is the period in which the climatic conditions are favourable for the growth and production of a crop.

(a) Kharif season vegetables: These may also be called rainy season crops. These vegetables require hot and humid climate. The season tentatively starts from 7 June and lasts till 6 October every year. The sowing of seeds may be undertaken from mid -May to late July. Vegetables, like okra, cowpeas, cluster beans, etc., are examples of Kharif vegetables.

(b) Rabi or cool season vegetables: These may also be called cool or winter season crops as these vegetables require low temperature for growth. The season tentatively starts from 7 October and lasts till 6 February. The sowing of seeds may be undertaken from mid-September to late October. Vegetables, like peas, radish, carrot, cauliflower, cabbage, knol-khol, leafy vegetables, etc., are examples of Rabi

vegetables.

(c) Summer or warm season vegetables: The season tentatively starts from 7 February and lasts till 6 June. The sowing of seeds may be undertaken from mid-January to late February. These crops require hot and dry climatic conditions for better growth and maximum production. Cluster bean, musk melon, cucumber, watermelon, etc., are summer season vegetables.

The diversity of physiographic, climatic and soil characteristics enables India to grow a large variety of horticultural crops. India is one of the world's largest producers of vegetables.

1. Orange:

Or Mandarin orange grows successfully in tropical and subtropical parts mainly under rain-fed conditions, in Coorg, Wayanad tract, Palani hills and the Nilgiris in the south between elevations of 600 and 1,500 m. Orange can be grown successfully on a wide range of soils, but the ideal soil is medium or light loam with a slightly heavier subsoil. Heavy black soil, underlain with murrain and having good drainage, is also suitable. In the hills and humid regions where planting is generally done on steep slopes, the land is properly terraced. In the plains, where the trees have to be irrigated, the land should be levelled. The places of production of oranges are Assam, Nagpur, Punjab, Wynaad, Coorg, Palani hills and the Nilgiris.

2. Mango:

Nearly 50 per cent of the total area under fruits in the country is occupied by mango. The mango tree grows throughout the country from the sea level up to about 1,500 m. It is adaptable to a wide range of soil and climatic conditions. It can withstand

both dry conditions and heavy rainfall. The mangos is a native of monsoon lands and prefers a climate with 75-250 cm rainfall concentrated from June to September and mean shade temperatures of about 28 °C. The maximum production of mangoes in India comes from Uttar Pradesh, Bihar, Andhra Pradesh, Maharashtra, Tamil Nadu, and Kerala among others. The important varieties grown include Chausa, Safeda, Langra, Dasheri of Uttar Pradesh and Bihar, Alphonso of Maharashtra and Goa, Banganapally of Andhra Pradesh, Totapari and Kesar of Gujarat, Rumani and Neelam of Tamil Nadu and Karnataka.

3. Grape:

Being a subtropical fruit grows well in dry climate having a short sharp winter and a long dry summer. They do not thrive in regions having humid summers. Grape grows best on light, friable, loamy soils with free drainage. Heavy soils are unsuitable. There are different varieties grown in different regions. In the northern plains common varieties are Black Prince, Bedana, Foster's seedling, Khandhari Dakh and Muscat of Alexandria and Perlette; in dry and temperate regions there are the Thompson seedless, Sultana and Kishmish white; in South India, Bangalore blue, Pachadraksha, Gulabi, Black Champa and Thompson seedless are grown; in western India, Cheema Sahebi, Anab-e-Shahi, and Thompson seedless are grown. The main places of production of grapes are in Punjab, Uttarakhand, Himachal Pradesh, Andhra Pradesh, Maharashtra, Karnataka and Tamil Nadu.

4. Banana:

Which is a moisture and heat loving plant, is broadly of two types table and culinary. Among the former are Poovan in Chennai (also known as Karpura Chakkarekeli in Andhra Pradesh); Mortaman, Champa and Amritsagar in West Bengal; Champa and

Mortaman in Assam and Orissa; Safed Velchi, Lai Velchi and Rajeli in Maharashtra. Among the culinary are Nandran, Monthan, Myndoli and Pacha Montha Bathis. Bananas are mainly grown in the tropical parts where temperatures do not fall below 16 °C and rainfall below 150 cm. The coastal plains and the irrigated tracts in the peninsular parts provide ideal climate for banana cultivation. The plant grows best in the rich well drained soil with ample moisture and humus content.The maximum production comes from three states—Maharashtra, Tamil Nadu and Kerala.

5. Guava:

Is a very hard tree which can withstand heat and droughts? A cool winter induces heavy fruiting. The total area under guava is about 30,000 hectare and Uttar Pradesh has the largest area under guava followed by Bihar.

6. Pineapple:

Is a humid tropical plant and grows well both in the plains and also at elevations not exceeding 900 m. It grows in all types of soils but can tolerate neither very high temperature nor frost. Assam, Meghalaya, West Bengal, Tripura, Uttar Pradesh, Andhra Pradesh, Kerala and Karnataka are the important places of production of pineapple.

7. Cashew:

Crop is grown mainly in peninsular India both for its fruits as well as for its nuts, mainly for the latter. It was in 16th century that the cashew plantations were introduced in India by the Portuguese. However the first seeds were brought from Brazil. Cashew cannot tolerate severe summers or winters. It requires a moderately high temperature of about 20 °C and a rainfall varying from 50 to 400 cm. It is not very exacting in soil requirements, as it grows even in very gravelly soils) Continued

adequate soil moisture is however necessary for the success of a cashew plantation.The fruits ripen from March to May but the season is extended in years when heavy rainfall is experienced in November-December. Cashew is commonly grown in the coastal districts of Kerala, Karnataka, Goa and Maharashtra. There are plantations on the east coast of Tamil Nadu, Orissa, West Bengal and Pondicherry. Tripura produces some cashews, too.

8. Mushroom:

Production has taken a quantum leap in the last few years. Mushrooms produce high quantity and quality protein from agro-wastes. It is rich in lysine (an aminoacid deficient in cereals).

The major variety in India is white button mushroom. Now growers in Central and Southern India are growing oyster mushrooms; Orissa and Kerala are growing paddy straw mushrooms.

Till 1980 Jammu and Kashmir and Himachal /Pradesh were producing mushroom (the white button variety being a temperate variety). Now Tamil Nadu, Uttarakhand, Uttar Pradesh, Haryana, Punjab and many other states have begun production with the introduction of other varieties.

9. Vegetables:

Constitute an important item of human diet throughout the world. Hence, the level of vegetable production in a country has an important bearing on the nutritional status of that country. A positive factor in cultivation of vegetables is that most of the vegetables are short-duration crop. As a result, they can be produced in succession, on the same plot and all the family labour of the vegetable grower can be usefully

employed throughout the year.

More than fifty varieties of vegetables are grown on an area of about four million hectare in India, major vegetable crops of the country include potato, onion, peas, cauliflower, tomato, brinjal, okra, cabbage and cucurbites.

Floral initiation includes all of the developments necessary for the irreversible commitment by the meristem to produce an inflorescence (Kinet JM. 1993. Environmental, chemical, and genetic control of flowering. Horticultural Reviews 15, 279–33). Control of floral initiation is not restricted to the developing meristem, but may involve signals from other areas of the plant. Autonomous flowering is where internal developmental cues lead to floral initiation. Floral induction is where an environmental stimulus, most commonly photoperiod or temperature, leads to floral initiation. Often, interactions between environmental stimuli and endogenous developmental cues exert some control over floral initiation. Some aspects of flowering in trees make them especially challenging for physiologists, breeders, and growers; first, the juvenile phase, which lasts for several years during which time no flowering or fruiting occurs; second, interactions between vegetative growth, flowers, and fruit of the previous year on floral initiation in the current year, affect growers through phenomena such as biennial bearing, and make interpretation of research data difficult for scientists.

**Floral initiation in Arabidopsis thaliana (L.) Heynh, and other herbs and grasses:**

Arabidopsis is a model plant used extensively for studying the molecular biology and genetics of flowering. Arabidopsis is particularly useful because the entire genome has been sequenced, and it is an easily transformable plant with a short life cycle that produces many seeds. The genetic diversity available through different ecotypes,

the winter annual and summer annual, and through a large range of mutants, is also useful to researchers. Four major pathways have been shown to lead to flowering in Arabidopsis: photoperiodic, autonomous, gibberellins (GA), and vernalization, and their actions at the genetic level have been revealed to a large degree. Flowering in Arabidopsis can be enabled by regulation of the expression of repressors, or actively promoted by endogenous or environmental signals (Boss et al., 2004). These pathways eventually converge by regulating the floral meristem identity genes (Pineiro and Coupland, 1998).

Photoperiodic induction Photoperiod is sensed in the leaves, with long-day (LD) and short-day (SD) plants flowering in response to the change in the dark period, requiring short and long dark periods, respectively. In Arabidopsis, CONSTANS (CO) mRNA expression is regulated by the circadian clock and peaks toward the end of the day (Suarez-Lopez et al., 2001). Under LD conditions the photoreceptors cryptochrome 1 and 2 and phytochrome A act antagonistically to phytochrome B to stabilize the CO protein, allowing it then to up-regulate FT (Valverde et al., 2004). Both CO and FT proteins are expressed specifically in the vascular tissues of the leaf (Takada and Goto, 2003). Once expressed, the FT protein is then transported via the phloem to the meristem (Corbesier et al., 2007), so that in Arabidopsis at least, the FT protein acts as a ‘florigen’. FD is a bZIP transcription factor that is preferentially expressed at the shoot apex. FT forms a protein complex with FD in order to interact with floral meristem identity genes such as APETALA 1 (AP1) (Abe et al., 2005; Wigge et al., 2005). Together or individually the floral meristem identity genes convert shoot meristems into flowers (Pineiro and Coupland, 1998). Genes homologous to FT have been found in several other species and, as for Arabidopsis, their proteins appear to fulfil the role of ‘florigen’. For example, in rice, Oryza sativa L.,

a SD plant, Hd1 is a CO orthologue and an output of the circadian clock, which promotes or suppresses FT orthologues under SD and LD conditions, respectively (Izawa et al., 2008). Under inductive conditions Hd3a mRNA, an FT orthologue, accumulates in the leaf blade and the protein is transported to the shoot apical meristem (SAM) where it promotes flowering (Tamaki et al., 2007). FT orthologue proteins have also been implicated as 'florigens' in cucurbits (Lin et al., 2007) and tomato (Lifschitz and Eshed, 2006).

GA floral induction The GA pathway also actively promotes flowering in Arabidopsis. Under SD conditions, GA4, which is most likely produced in the leaves and transported to the meristem, up-regulates one or both of the genes LEAFY (LFY), a floral meristem identity gene (Blazquez et al., 1998; Eriksson et al., 2006), and SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1 (SOC1), a 'floral integrator' (Bernier and Perilleux, 2005), leading to flowering. GA-deficient mutants have delayed flowering under short days but flower on time under long days (Wilson et al., 1992). However, double mutants of the photoperiodic and GA pathways flowered later under long days than double mutants of the photoperiodic and autonomous pathways (Reeves and Coupland, 2001), suggesting some interaction between the photoperiodic and GA pathways. The interactions between photoperiodic induction and GA are well understood in Lolium temulentum L., a LD flowering grass. Long days cause up-regulation of GA biosynthesis genes in the leaves, an increase in GA concentrations in the leaves, and an increase in GA export to the SAM (King et al., 2006). The L. temulentum homologues of Arabidopsis' CO (LtCO) and FT (LtFT) also respond to long days with increased transcription levels in the leaves. Importantly, exogenous applications of GA to the leaves in SD conditions resulted in flowering without increasing LtFT levels. King et al. (2006) concluded that GA was acting as a

‘florigen’ and that LtFt could either act as a ‘florigen’ or enable the production and transport of other signals. While GA plays an important role in promotion of flowering in both Arabidopsis and L. temulentum, only in L. temulentum has it been shown to act as a ‘florigen’ in response to photoperiodic induction.

Vernalization Flowering in response to exposure to cold temperatures, –1 C to 10C, for extended periods is termed vernalization (Simpson and Dean, 2002). Variation at the FRIGIDA (FRI) locus appears to be the main determinant of flowering time in accessions of Arabidopsis with the winter annual habit, that is, those that require vernalization; dominant alleles of FRI require vernalization while many early flowering types carry the non-dominant fri allele (Gazzani et al., 2003). FRI acts to suppress flowering by increasing the levels of FLOWERING LOCUS C (FLC) mRNA, but may also act to suppress flowering through pathways independent of FLC (Michaels and Amasino, 1999). FLC is a MADS domain gene (Michaels and Amasino, 1999). MADS domain genes are a large group and have a range of plant developmental functions, although those associated with flowering have been most commonly investigated. Variation in FLC also confers variation in the vernalization phenotype; in late flowering FLC mutants (FLC is over expressed), vernalization speeds up flowering and reduces the expression of FLC to undetectable levels. FLC represses expression of SOC1, which prevents up-regulation of FD in the meristem (Searle et al., 2006). FLC also inhibits transcription of FT in the leaf (Searle et al., 2006); therefore vernalization is sensed in both the leaves and meristem to suppress expression of FLC. Vernalization is also well understood in winter cereals, barley (Hordeum vulgare) and wheat (Triticum aestivum) in particular. Vernalization hastens flowering by promoting expression of the VRN1 gene (Trevaskis et al., 2003), a floral integrator related to APETALA1 in Arabidopsis (Yan et al., 2004), which down-regulates the

floral repressor VRN2 (Trevaskis et al., 2006). Flowering is hastened in wheat and barley in long days through VRN3 expression (an FT homologue) (Turner et al., 2005). It has been proposed that in genotypes requiring vernalization, VRN2 expression prevents flowering in long days until after vernalization (Trevaskis et al., 2007).

Autonomous flowering the autonomous pathway also acts upon the expression of FLC although independently of vernalization. In this case, several genes act additively to suppress the expression of FLC (Michaels and Amasino, 1999), but it is unclear why they act at particular stages of plant development (Boss et al., 2004). The autonomous pathway may also assist the photoperiodic and GA pathways through its action upon the floral repressors (Reeves and Coupland, 2001). In addition to these four floral pathways the flowering of Arabidopsis appears to be regulated by more general aspects of plant metabolism (Bernier and Perilleux, 2005). For example, Corbesier et al. (1998) found that sucrose was important both as a signal and assimilate in the flowering of a starchless mutant; Eriksson et al. (2006) found that sucrose could act synergistically with GA to promote flowering in the absence of long days; and Bagnall and King (2001) reported that there were complex interactions between light quality and quantity and the availability of assimilates during LD induction.

Case study 1: floral induction in mango

Mango, Mangifera indica L., is an evergreen tropical tree cultivated in the tropics and subtropics. With respect to floral initiation, mango has been more extensively researched than any other tropical tree species. The juvenile period for mango varies with cultivar but can be approximately three years for particular cultivars (Salomon and Reuveni, 1994). Floral initiation occurs during late autumn and early winter; flower panicles emerge from the terminal and sub-terminal buds and grow

continuously until anthesis occurs in the spring (Fig. 2). Most mango cultivars bear irregularly. This has been largely attributed to variation in flowering and, in subtropical areas, fruit retention (Whiley, 1993). Variations in the amount of flowering may be within trees from year to year, between trees in the same year, and between branches on the same tree. Some Indian cultivars are reputedly biennially bearing, having distinct 'on' and 'off' years (Pandey, 1989).

Many of the cultivars grown in Australia, including 'Kensington Pride', flower irregularly, but without predictable 'on' and 'off' years (Blaikie and Kulkarni, 2002). Under subtropical conditions mango flowers in response to cool temperatures (Whiley et al., 1989; Batten and McConchie, 1995; Shu and Sheen, 1987; Chaikiattiyos et al., 1994; Nunez-Elisea and Davenport, 1994), although the temperatures reported for cool temperature induction in mango are much higher than those reported for vernalization of Arabidopsis above. Whiley et al. (1989) found that eight out of ten mango cultivars flowered at a day/night temperature regime of 15/10 C, and only one of the cultivars flowered at 20/15 C, while the other nine cultivars grew vegetatively; and Shu and Sheen (1987) found that 100% of 'Haden' mangoes flowered at 19/13 C, 60% at 25/19 C and 0% at 31/25 C. Interestingly, four cultivars that flowered at 30/20 C in the work of Sukhvibal et al. (2000) failed to flower at 20/15 C in the work of Whiley et al. (1989). It is possible that the larger diurnal temperature difference was a significant factor, as speculated by Batten and McConchie (1995) for lychee (Litchi chinensis Sonn.). Reports on the duration of cold temperature needed for floral initiation vary from 4 d (Reece et al., 1946) to 2 weeks (Shu and Sheen, 1987) in cultivar 'Haden' and up to 35 d in 'Tommy Atkins' and 'Keitt' (Yeshitela et al., 2004). There is evidence for a phloem mobile floral stimulus (florigen) in mango. Kulkarni (1986, 1988b, 1991) examined mango

flowering by cross-grafting cultivars with different inductive requirements. While the rootstock was under inductive conditions it could promote flowering in the defoliated scion under conditions non-inductive for the scion cultivar, so long as the rootstock had leaves. However, when leaves remained on the scion, flowering was inhibited and subsequent growth was vegetative. Similarly, juvenile mango plants have the ability to flower after grafting to a mature plant so long as the juvenile plant is defoliated and the adult plant has leaves (Singh, 1959), indicating signals from the leaves of the adult plant promote flowering and can overcome juvenility, while leaves from juvenile plants inhibit flowering. In separate studies, when branches were girdled and decapitated, the growth from axillary buds was floral if leaves were allowed to remain on the plant for more than 4 d under inductive conditions (Reece et al., 1946, 1949). Floral initiation will occur in the presence of even a fraction of a mature leaf, but the proportion of stems initiating reproductive, as opposed to vegetative, growth decreases with increasing distance from the leaves, and as the number of leaves decreases (Davenport et al., 2006). From these observations, there seems to be a floral stimulus in mango that is transient, graft transmissible, and generated by the leaves. Vegetative growth in mango is through episodic flushing, which is more frequent as temperature increases (Whiley et al., 1989). Episodic or recurrent flushing, common in subtropical and tropical trees, is where apical or axillary buds are released and the new shoots expand continuously through several nodes and then mature. After a period of dormancy, the cycle begins again with further bud release. The timing of flush development is important for successful flowering because bud release, for vegetative or reproductive growth, can only occur from mature flush (Nunez-Elisea and Davenport, 1995). In addition, buds appear to be receptive to the floral stimulus for only a small portion of the flush development

cycle, because floral induction seems to require inductive temperatures approximately to coincide with bud release. Recently emerged buds on plants of cultivar 'Irwin', growing in warm, non-inductive conditions initiated flower panicles when they were moved to florally inductive ambient winter conditions, so long as the buds were less than approximately 10 mm in length (Batten and McConchie, 1995). Treatments such as pruning that manipulate the timing of flush development and synchronize canopy flushing have been successful in increasing flowering intensity (Yeshitela, 2005). Under tropical conditions, in which cold inductive temperatures may be brief, erratic or non-existent in some seasons, it is unclear what exactly leads to floral initiation; however, some factors improve the likelihood of flowering. First, some cultivars flower more reliably than others (Pandey, 1989) and will flower at higher temperatures. For example 'Florigon' was the only cultivar to flower at the higher temperature treatment of 20/15 C of ten cultivars tested by Whiley et al. (1989). Second, treatments which reduce vegetative vigour such as paclobutrazol (GA biosynthesis inhibitor), and manipulate the timing of flush development, such as water stress (Davenport, 2003), may help if they serve to focus bud release around the time of inductive temperatures, although this requires testing. Water stress may be used only indirectly to promote flowering, as described below for lychee. Experimentally, water stress per se has not been shown to induce flowering or decrease the cold requirement of mango (Chaikiattiyos et al., 1994; Nunez-Elisea and Davenport, 1994). Third, potassium nitrate is thought to induce flowering (Bondad and Apostol, 1979), but seems to be ineffective in many environments (Davenport and NunezElisea, 1997). There is some correlative evidence for regulation of floral initiation in mango by plant growth regulators (PGRs), GA in particular. Evidence comes from measurements of endogenous GA, the effects of exogenous GA, and

the effects of GA biosynthesis inhibitors. The concentration of GA in terminal stems of cultivar 'Khiew Sawoey' decreased during the 16 weeks before panicle emergence in trees that subsequently flowered, and increased over the same period in terminal stems of trees that remained vegetative (Tongumpai et al., 1991). This raises the possibility of a direct inhibitory role of GA in mango floral initiation. Exogenous applications suggest that GA may indirectly regulate mango flowering by delaying bud release, because applied GA delays bud release and does not inhibit flowering so long as bud release occurs under florally inductive conditions (Nunez-Elisea and Davenport, 1998). GA biosynthesis inhibitors such as paclobutrazol (Rademacher, 1995) both hasten and increase the flowering intensity of mango (Kulkarni, 1988a; Blaikie et al., 2004) and also reduce vegetative vigour (Winston, 1992). So paclobutrazol may directly promote flowering, or act indirectly by increasing the likelihood of bud release during floral inductive conditions. Therefore, GA may inhibit floral initiation endogenously or may act indirectly by influencing the timing of bud release. In summary, the only factor shown experimentally to induce flowering in mango is temperature below 15–20 C, with florally inductive temperatures varying between cultivars. Floral initiation is affected by the cycle of flush development, and the timing and intensity of flowering can be manipulated by exogenous applications of PGRs. The evidence for the internal regulation of floral initiation by GA is not conclusive.

Case study 2: floral initiation in apple

Apple is a temperate, deciduous tree grown commercially from the tropics to high latitude temperate regions (Lakso, 1994). Apple has a long juvenile phase which can be greater than six years; however, grafting onto dwarfing rootstocks can reduce the juvenile phase (Kotoda et al., 2006). Spring bloom in apple is part of the cycle of

reproductive development that begins with floral initiation in the preceding summer (Abbott, 1970). The process is not continuous, but broken by the period of rest associated with the winter months, during which no development occurs. The apple inflorescence is a determinate raceme which often has five flowers (Westwood, 1978). Apple is an autonomous flowering plant, as are many other temperate deciduous tree crops. Apple flowers are borne on two types of shoots, spurs and long shoots (Fig. 3). The spur is a short shoot in which extension growth is limited to the production of a rosette with few leaves (Abbott, 1970). The axis of the spur is called the 'bourse' which can continue to produce short shoots from the axillary buds in the following seasons (Luckwill, 1970). Long shoots are the extension shoots of the current season's growth, and, particularly in new cultivars, can produce flowers from both terminal and axillary buds (Tromp, 2000). Meristems of developing vegetative buds include several appendages: bud scales, bracts, transition leaves, and true leaves. The vegetative buds must be fully developed for the transition to floral buds to occur (Buban and Faust, 1982). The appendages begin developing when growth resumes in spring. A critical appendage (node) number in vegetative buds was suggested by Fulford (1965, 1966a) and reported as 16 for 'Golden Delicious' (Luckwill and Silva, 1979). Attainment of the critical node number appears to be the prerequisite for a bud to make the transition from vegetative to floral; no compelling reason can be cited but there is experimental evidence supporting this critical node requirement (Luckwill and Silva, 1979; Hirst and Ferree, 1995; McArtney et al., 2001; Bertelsen et al., 2002). The rate of node development needs to be fast enough to ensure the critical node number is reached before the end of the growing season; this is most important at high latitudes with short growing seasons (Faust, 1989). The first sign of transition from vegetative to reproductive growth is doming

of the apical meristem which, in spurs, may occur approximately 50 d after full bloom (Kotoda et al., 2000; Foster et al., 2003). Lateral floral meristems and bracts then develop until the terminal and lateral flowers have initiated sepals (Foster et al., 2003), this differentiation may continue throughout the autumn until the onset of winter dormancy (Sung et al., 2000). The flowers are completed after the release of dormancy between bud burst and anthesis (Sung et al., 2000). Environmental conditions exert some control over floral initiation in apple. Heat unit accumulation could not consistently account for the timing of floral initiation in 'Royal Gala' (McArtney et al., 2001), but the temperature during the growing season can affect the intensity of floral initiation and it may be that temperatures which induce high vegetative vigour reduce floral initiation (Tromp, 1976, 1980). Low irradiance has been shown to inhibit floral initiation on spurs. Flowering on spurs was not affected at up to 30% shading but was totally inhibited when shading increased to 70% of the available light in cultivar 'McIntosh' (Cain, 1971).

Many cultivars of apple have a tendency to bear alternately. Heavy fruit loads accentuate biennial bearing by reducing flower production (Luckwill, 1970). Early work also demonstrated that reducing fruit load could increase flower production and that the effect was reduced the longer fruit removal was delayed (Harley et al., 1942). On individual spurs, increased bourse shoot length and increased leaf area were found to increase flowering (Neilsen and Dennis, 2000), while defoliation (Ramirez and Hoad, 1981) and the presence of fruit diminished flowering (Fulford, 1966b). There is evidence that the inhibitory effect of fruit load on flowering is due to GA export from the seeds. Luckwill (1970) noted high levels of GA in apple seeds during embryo growth from approximately 5 weeks to a maximum at 9 weeks after full bloom. The inhibitory effect of seeds on flower production was demonstrated by

experiments using the cultivar ‘Spencer Seedless’ that can be manipulated to produce seedless or seeded fruit; seeded fruit inhibited flower production on spurs while seedless fruit did not (Chan and Cain, 1967; Neilsen and Dennis, 2000). GA inhibit floral initiation in apple (Tromp, 1982; McLaughlin and Greene, 1984; Bertelsen et al., 2002). GA may act by reducing the rate of node development; GA application in ‘Pacific Rose’ reduced bud appendage production, bud size, and both delayed and reduced the transition of buds from vegetative to floral (Bertelsen et al., 2002). While GA inhibit flowering, cytokinin can promote flowering when applied soon after full bloom (McLaughlin and Greene, 1984). Cytokinin application as zeatin increased flowering on spurs and replaced the need for leaves in floral initiation on defoliated spurs (Ramirez and Hoad, 1981). Other plant growth regulators also affect floral initiation in apple. For example, daminozide increases flower bud formation (Ramirez and Hoad, 1981; McLaughlin and Greene, 1984), and has been reported to both decrease GA tissue concentrations (Hoad and Monselise, 1976) and increase cytokinin tissue content (Ramirez and Hoad, 1981). Ammonia increased floral initiation and stem arginine content when applied as a four mM ammonium sulphate nutrient solution (Rohozinski et al., 1986). Orthologues of floral meristem identity genes and MADS domain genes of Arabidopsis have been identified in apple. Two orthologues of LEAFY named AFL1 and AFL2 were isolated from cultivar ‘Jonathan’ and were subsequently shown to hasten flowering in transformed Arabidopsis plants (Wada et al., 2002). Further, expression of AFL1 in the apple meristem began when phenotypic transition of buds from vegetative to floral was observed. Two members of the MADS domain gene family, similar to AGL2 and AGL4 from Arabidopsis, have been isolated in cultivar ‘Fuji’. Both were expressed in the early stages of flower development and one was expressed during the later stages (after dormancy) (Sung

et al., 2000). The apple gene MdTFL1 delayed flowering in transformed Arabidopsis plants (Kotoda and Wada, 2005), and transformed 'Orin' apple plants expressing antisense MdTFL1 RNA flowered as little as 8 months after transfer to the greenhouse, compared with the nontransformed control plants that did not flower in 6 years, indicating that MdTFL1 has a role in maintaining the juvenile phase in apple (Kotoda et al.. 2006). Some of the early flowering transgenic MdTFL1 antisense expressing plants had continuous flowering habits and altered branch architecture due to varying flower positions, indicating additional roles of MdTFL1 in the timing and location of floral initiation. Upstream regulation of these apple flowering genes by the environment or endogenous signals is not understood. Research investigating floral initiation in apple implicates seasonal developmental processes and hormonal relationships as the major factors driving floral initiation as opposed to specific environmental stimuli.

Other tree crops

Environmental control of floral initiation A range of subtropical and tropical tree species can be induced to flower by exposure to low temperature: mango, lychee (Menzel and Simpson, 1995), macadamia (Macadamia integrifolia Maiden and Betche) (Nakata, 1976), avocado (Persea americana Mill.) (Buttrose and Alexander, 1978) and orange (Citrus sinensis L.) (Moss, 1976). Olive (Olea europaea L.), an evergreen tree generally grown in Mediterranean environments, can also be induced to flower under cool conditions (Hackett and Hartmann, 1964). One major difference between cool temperature induction in subtropical and tropical trees, and vernalization in herbaceous species, is the temperature required: subtropical and tropical trees often require temperatures around 15–20 C whereas vernalization in herbaceous species requires temperatures between –1 C and 10C. With respect to

temperate deciduous species, high temperatures (up to 30 C) increased inflorescence production in grapevine, Vitis vinifera L., while temperatures of 21 C and below increased tendril production (Buttrose, 1970), but for southern high bush blueberry (Vaccinium corymbosum L.), 28 C inhibited floral induction compared with 21 C (Spann et al., 2004). Therefore cool temperatures induce flowering in several tropical and subtropical horticultural trees. In temperate deciduous horticultural trees, temperature can affect the intensity of floral initiation, but it is not clear if temperature provides an inductive stimulus. The site of perception of cool florally inductive temperatures has not been extensively investigated. In mango, cool temperatures may be sensed in the leaves because mature leaves appear to be the source of an essential floral stimulus (described above in the mango case study). Lychee may be similar given that mature leaves also appear necessary for floral initiation (Menzel et al., 2000; Ying and Davenport, 2004). However high root temperatures can inhibit floral initiation in lychee even when shoots are exposed to florally inductive temperatures (O'Hare, 2004), implicating either perception by the roots and long-distance signalling or heat transfer via the transpirational stream. In citrus, in contrast, leaves are not necessary for floral initiation in cool inductive temperatures (Davenport, 2000) or for floral induction via water stress (Southwick and Davenport, 1986), indicating that both the cold temperature and water stress stimuli that induce flowering may be perceived in the stem or buds. Photoperiodic induction, a common mechanism in herbaceous species, has rarely been demonstrated in trees. Southern high bush blueberry flowers in response to short days of 8 h, but not under long days or short days with a 1 h night interruption (Spann et al., 2003); this is most likely a response to photoperiod. In avocado, both the time to flowering and floral initiation were decreased by short days of 9 h compared with

15 h (Buttrose and Alexander, 1978), but these effects may be related to differences in photosynthetic period and daily carbon assimilation rather than to photoperiod. Light intensity also influences floral initiation in perennials; as described for apple above. In kiwi fruit, Actinida chinensis Planch., shaded shoots produced fewer floral buds and fewer inflorescences per shoot than exposed shoots (Grant and Ryugo, 1984). In olive, both high and low light intensity treatments reduced floral initiation (Stutte and Martin, 1986). Similarly in the ornamental tree, Metrosideros excelsa Soland. ex Gaertn., the greatest flowering intensity occurred at intermediate light intensities (Henriod et al., 2003). Although variations in light intensity can affect floral initiation quantitatively, it is most likely not an inductive stimulus in these cases but a secondary factor perhaps related to assimilate production and its effects on growth. Water stress has been demonstrated to induce flowering experimentally in two citrus horticultural tree species. Tahitian limes, Citrus latifolia Tan., flowered on resumption of daily irrigation after both cyclic and constant water stress for as little as 2 weeks (Southwick and Davenport, 1986). When the same Tahitian lime plants had completed a vegetative flush 2 months later, water stress and subsequent resumption of adequate watering resulted in floral initiation again. Rewatering following water stress also caused floral initiation in lemon, Citrus limon (L.) Burm. f., but not in lychee, mango or avocado (Chaikiattiyos et al., 1994). It is not clear if the inductive stimulus is provided by the period of water stress or the subsequent watering. Water stress can also act indirectly to promote floral initiation by checking vegetative flushing, as demonstrated for lychee (Stern et al., 1998).

Vegetative growth and floral initiation Horticultural tree species vary both in the types of shoots that produce flowers and where on these shoots the flowers are borne. The location of the flowers and the timing of floral initiation influence how

flowering and vegetative growth interact. Several subtropical species, including lychee, tend to produce inflorescences from terminal buds; others, such as avocado, from both terminal and axillary buds; and still others, like macadamia, Macadamia integrifolia Maiden and Betche, M. tetraphylla Johnson, and hybrids, from axillary buds. Similar to apple, several other temperate deciduous species, such as pear, Pyrus communis L. (Faust 1989), and sweet cherry, Prunus avium L. (Webster and Shepherd, 1984), initiate flowers on specialized spur structures as well as on current season's growth. On the other hand, peach, Prunus persica L. Batsch (Dorsey, 1935), and apricot, Prunus armeniaca L., (Jackson, 1969), initiate flowers in lateral buds of the current season's growth. In the subtropical trees lychee, avocado, and macadamia, flowering is dependent on bud release during cool florally inductive temperatures (Olesen, 2005). This is largely regulated by maturity of the most recent flush (discussed below), but the likelihood of bud release and flowering can also be affected by characteristics of the shoot, as for macadamia (JD Wilkie et al., unpublished data). In temperate deciduous species, however, the release of pre-existing floral or vegetative buds in the spring after winter dormancy is dependent on satisfying the chilling requirements (Rohde and Bhalerao, 2007).

Vegetative growth in lychee is through recurrent flushing, with the interval between successive flushes dependent on the prevailing weather conditions (Olesen et al., 2002). There is only a small part of this cycle when the new shoots are receptive to floral induction, that being around the time of early flush development when the expanding buds are no more than a few millimetres in length (Batten and McConchie, 1995). Therefore, vegetative shoots that are not mature by late autumn often do not flower, because the cyclic nature of flush development means they will initiate new growth only after cool florally inductive winter conditions have passed. Macadamia is

similar except that the cycle of flush development generally affects the flowering behaviour of mature shoots at a distance from the most recent apical flush instead of the flowering behaviour of the most recent apical flush itself (Olesen, 2005). Avocado is also similar, and intermediate to lychee and macadamia in its flowering behaviour (Olesen, 2005). The timing of vegetative growth also affects floral initiation in some temperate deciduous tree crops, where floral initiation occurs in the growing season before anthesis. In grapevine, the undifferentiated primordia have the potential to produce inflorescences or tendrils depending on their location and climatic conditions; inflorescences tend to be formed in developing latent buds and tendrils in growing shoots (Boss et al., 2003). Floral initiation in peach is also reliant on, but not inhibited by, vegetative growth; floral initiation occurs in buds of the current season's growth and begins when the buds are approximately four nodes back from the growing tip (Dorsey, 1935). Excessive vegetative growth has often been cited as being antagonistic to flower bud initiation in apple and some other temperate fruit trees (Luckwill, 1974; Faust, 1989; Forshey and Elfving, 1989). Consistent with this, dwarfing rootstocks increase early flowering of apple (Luckwill, 1974); growth retardants such as daminozide can increase flower bud initiation of apple (McLaughlin and Greene, 1984); and for sweet cherry, as regrowth in response to pruning increases, floral initiation decreases (Guimond and Andrews, 1998). However, treatments that increase vigour do not always decrease floral initiation; greater shoot growth due to increasing temperatures (20 C compared to 13 C) during the growing season also increased flower bud initiation of apple (Zhu et al., 1997). These inconsistencies may be due to effects of the treatments that are independent of vigour, for example, dwarfing rootstocks may induce early flowering independent of their effect on vegetative growth; or high temperature during the growing season

may promote flowering independently of vegetative growth.

The role of plant growth regulators The literature on the role of GA in the floral initiation of woody perennials is vast and inconsistent. However, there is evidence to suggest that endogenous GA can inhibit floral initiation and that GA can also inhibit floral initiation through effects on shoot growth, as discussed for mango above. For example, applied GA inhibits floral initiation in avocado (Salazar-Garcia and Lovatt, 1998), citrus (Lord and Eckard, 1987), sweet cherry (Lenahan et al., 2006), and peach (Garcia-Pallas and Blanco, 2001); reduced levels of endogenous GA have been correlated with floral initiation in citrus (Koshita et al., 1999), lychee (Chen, 1990); and GA biosynthesis inhibitors have improved flowering in mango (Winston, 1992), and lychee (Menzel and Simpson, 1990), and macadamia (Nagao et al., 1999). Floral initiation in grapevine occurs in uncommitted primordia of developing latent buds destined for dormancy and subsequent release in the following spring (Srinivasan and Mullins, 1980). The uncommitted primordia have the potential to produce tendrils as well as inflorescences, but tendrils tend to be produced only when uncommitted primordia initiate growth in the same season in which they were produced, that is, without undergoing winter dormancy (Boss et al., 2003). However, in a dwarf, GA-insensitive mutant of grapevine, only inflorescences and no tendrils were produced from uncommitted primordia of the expanding shoots (Boss and Thomas, 2002). Thus endogenous GA appear to inhibit floral initiation in grapevine. GA applications in citrus that inhibit flowering reduce the number of buds that are released in spring but not the proportion of buds that produce floral shoots (Garcia-Luis et al., 1986). Thus the effect seems to be on shoot growth rather than floral initiation. Applied GA also affects shoot growth in apple by reducing the rate of node development, lessening the chances of the buds reaching the critical appendage

number (Bertelsen et al., 2002). The presence of fruit inhibits floral initiation in several species including the pome fruits (Weinbaum et al., 2001) and citrus (Garcia-Luis et al., 1986). Large crops can lead to poor floral initiation in the following year and induce a cycle of biennial bearing. GA exported from the seeds of pome fruits (Chan and Cain, 1967) and some part of citrus fruit to the buds (Garcia-Luis et al., 1986) is thought to be involved in the inhibition. Cytokinins may also be involved in floral initiation. Endogenous cytokinin levels in buds of lychee increase at the onset of florally initiation and differentiation, and exogenous applications increase floral initiation (Chen, 1991), although there is no evidence that cytokinins can replace the florally inductive stimulus. Application of the growth retardant maleic hydrazide to 'Japanese pear', Pyrus pyrifolia Nakai, increased both endogenous cytokinin levels and floral initiation (Ito et al., 2001). Ethylene has long been used to promote flowering commercially in pineapple (Ananas comosus (L.) Merr.) (Turnbull et al., 1999); there are also indications that it promotes flowering in apple (Bukovac et al., 2006). More comprehensive accounts on the role PGRs in floral initiation of several horticultural trees are available, including apple (Buban and Faust, 1982; Dennis and Neilsen, 1999), mango (Davenport and Nunez-Elisea, 1997), and citrus (Davenport, 1990).

The role of carbohydrates Carbohydrates have two roles in plant development, in the general provision of energy and carbon skeletons for growth and in the regulation of metabolism. The challenge for research into floral initiation is in designing experiments that separate out these roles. In the LD flowering perennial shrub Fuchsia hybrida Hort. ex Sieb. & Voss, floral induction can occur in the presence of long days or high irradiance short days (King and Ben-Tal, 2001). The extent of floral initiation under high irradiance SD conditions is correlated with the sucrose

concentration at the apex, and under these conditions sucrose may be acting as a florigen. This is not so for LD induction because the sucrose concentration did not increase at the apex with the increase in daylength (King and Ben-Tal, 2001). As a perennial shrub, F. hybrida is somewhat removed from horticultural trees but does demonstrate a potential direct effect of carbohydrates in floral signalling in a perennial species. The need for carbohydrates for floral initiation has often been investigated by measuring levels of stored carbohydrates, or imposing treatments such as girdling that modify the levels of stored carbohydrates, and correlating these with flowering intensity. The results have been mixed. Girdling increased flowering intensity in olive (Lavee et al., 1983), lychee (Menzel and Simpson, 1987), and citrus (Goldschmidt et al., 1985) indicating increased stored carbohydrates can increase floral initiation, because girdling has been reported to increase levels of stored carbohydrates in some horticultural trees (Goldschmidt et al., 1985; Menzel et al., 1995). Further, a study of stored carbohydrates in biennial bearing citrus found that high and low levels of stored carbohydrates corresponded with high and low levels of floral initiation, respectively (Goldschmidt and Golomb, 1982). However, other experiments with citrus have revealed complex interactions between cool inductive temperatures, PGRs, fruit load, and girdling treatments on the flowering intensity (Goldschmidt et al., 1985). In olive, both high and low light intensity treatments, in which high and low levels of stored carbohydrate were measured, respectively, resulted in decreased flowering relative to the control, and the effects of carbohydrate were minor compared with the inhibition of flowering due to the presence of fruit (Stutte and Martin, 1986). It is unclear whether increased flowering intensity in treatments that also increase the availability of carbohydrates in horticultural trees is due to the action of carbohydrates as a floral stimulus or an

energy source.

Flowering genes in horticultural trees Orthologues of Arabidopsis flowering genes have been identified in several tree species. Studies to determine the function of these genes generally involve correlation of gene expression with floral initiation/development or transgenic studies, where flowering genes from the perennial species are inserted into a related perennial species or Arabidopsis. In general, perennial flowering gene orthologues have been shown to function akin to their Arabidopsis namesakes. For example, Satsuma mandarin FT orthologue mRNA levels increased with the seasonal onset of cool temperatures during the time of floral induction (Nishikawa et al., 2007); there is evidence that LEAFY orthologues isolated from sweet orange (Pillitteri et al., 2004b) and grapevine (Boss et al., 2006) act as floral promoters; and evidence that TFL1 orthologues isolated from citrus (Pillitteri et al., 2004a) and grapevine (Bosset al., 2006) act as floral inhibitors. There is now some understanding of how the expression of flowering genes integrates with the environment and flowering time in horticultural trees. In the temperate deciduous tree poplar, Populus sp., FT orthologue expression increased in long days and appeared to be at least partly influenced by the timing of CO orthologue transcription; additionally, FT orthologue expression varied seasonally and corresponded to the timing of floral initiation in long days, while expression of an FT orthologue in young transformed poplar plants removed the juvenile phase (Bohlenius et al., 2006). In Satsuma mandarin, FT orthologue mRNA levels increased with the time spent under florally inductive conditions (Nishikawa et al., 2007). In sweet orange, LFY and AP1 orthologue RNA levels increased during and after florally inductive cool temperatures while RNA of the TFL orthologue was absent (Pillitteri et al., 2004a). In transgenic hybrid citrus, Citrus sinensis L. Osbeck3Poncitrus trifoliata

L. Raf., over-expression of LFY and AP1 orthologues substantially reduced the juvenile phase, but flowering still appeared to be under both environmental and endogenous control because it occurred only once a year in the spring (Pena et al., 2001).

## CONCLUSIONS

So far, the literature on floral initiation in herbaceous plants has been reviewed, in particular Arabidopsis, then mango, apple, and horticultural trees in general. It is apparent that floral initiation in trees is controlled by a range of factors which may include environmental stimuli, developmental cues, and other interactions with vegetative growth and PGRs. It is also apparent that rarely can one factor be considered in isolation. Annual plants, such as Arabidopsis, may have several pathways to flowering which include induction in response to environmental stimuli or autonomous initiation. Horticultural trees generally initiate flowers in response to either an environmental stimulus or autonomously. There is some evidence that the mechanisms through which environmental stimuli act are similar between annual plants and horticultural trees. For example, the roles of CO and FT in Arabidopsis appear to be similar to those of orthologues in poplar (Bohlenius et al., 2006) and the role of TFL1 in Arabidopsis appears to be similar to that of the orthologue in grapevine (Boss et al., 2006). However, there may also be differences. Vernalization acts on the meristem and leaves in Arabidopsis to suppress floral repressors, but in mango cool temperatures are sensed in the mature leaves which then generate a signal that is exported to the meristem to promote flowering. Thus the floral response to cool temperatures in mango appears to be more analogous to photoperiodic induction in Arabidopsis, or to the effects of ambient temperature on

genes of the autonomous flowering pathway (Blazquez et al., 2003). Two major differences exist between tropical and temperate deciduous horticultural trees with respect to floral initiation. First, tropical species such as mango initiate flowers in response to an environmental stimulus, while temperate deciduous species, such as apple, initiate flowers autonomously. Second, temperate deciduous horticultural trees undergo a period of dormancy between floral initiation and anthesis, while in tropical species, including mango, floral development is continuous from floral induction to anthesis. Notwithstanding these differences, the purpose is the same, flowering under environmental conditions suitable for successful reproduction. Tropical species such as mango and lychee often use a predictable environmental stimulus, cool winter temperatures, to induce flowering. Temperate deciduous species initiate flowers during the growing season but initiate growth in the following spring only after the chilling requirements of winter dormancy have been satisfied and temperatures are suitable for growth. Research in trees is expensive, slow, and has often been focused on limits to production in horticultural species. Recent advances in the understanding of the genetic control of floral initiation in herbaceous plants such as Arabidopsis have provided a platform from which trees can be studied.

## REFERENCES

Abbott DL. 1970. The role of budscales in the morphogenesis and dormancy of the apple fruit bud. In: Luckwill LC, Cutting CV, eds. Physiology of tree crops. New York: Academic Press, 64–82.

Abe M, Kobayashi Y, Yamamoto S, Daimon Y, Yamaguchi A, Ikedo Y, Ichinoko H, Notaguchi M, Goto K, Araki T. 2005. FD, a bZIP protein mediating signals from the

floral pathway integrator FT at the shoot apex. Science 309, 1052–1056.

Bagnall DJ, King RW. 2001. Phytochrome, photosynthesis and flowering of Arabidopsis thaliana: photophysiological studies using mutants and transgenic lines. Australian Journal of Plant Physiology 28, 401–408.

Batten DJ, McConchie CA. 1995. Floral induction in growing buds of lychee (Litchi chinensis) and mango (Mangifera indica). Australian Journal of Plant Physiology 22, 783–791.

Bernier G, Havelange A, Houssa C, Petitjean A, Lejeune P. 1993. Physiological signals that induce flowering. The Plant Cell 5, 1147–1155.

Bernier G, Perilleux C. 2005. A physiological overview of the genetics of flowering time control. Plant Biotechnology Journal 3, 3–16.

Bertelsen MG, Tustin DS, Waagepetersen RP. 2002. Effects of GA3 and GA4+7 on early bud development of apple. Journal of Horticultural Science and Biotechnology 77, 83–90.

Blaikie SJ, Kulkarni V. 2002. Manipulating flowering in mango, cv. Kensington Pride. Acta Horticulturae 575, 791–796.

Blaikie SJ, Kulkarni VJ, Muller WJ. 2004. Effects of morphactin and paclobutrazol flowering treatments on shoot and root phenology in mango cv. Kensington Pride. Scientia Horticulturae 101, 51–68.

Blazquez MA, Green R, Nilsson O, Sussman MR, Weigel D. 1998. Gibberellins promote flowering of Arabidopsis by activating the LEAFY promoter. The Plant Cell 10, 791–800. Blazquez MA, Hoon Ahn J, Weigel D. 2003. A thermosensory pathway controlling flowering time in Arabidopsis thaliana. Nature Genetics 33, 168–171.

Bohlenius H, Huang T, Charbonnel-Campaa L, Brunner AM, Jansson S, Strauss SH, Nilsson O. 2006. CO/FT regulatory module controls timing of flowering and seasonal

growth cessation in trees. Science 312, 1040–1043.

Bondad ND, Apostol CJ. 1979. Induction of flowering and fruiting in immature mango shoots with KNO3. Current Science 48, 591– 593.

Boss PK, Bastow RM, Mylne JS, Dean C. 2004. Multiple pathways in the decision to flower: enabling, promoting, and resetting. The Plant Cell 16, S18–S31.

Boss PK, Buckeridge EJ, Poole A, Thomas MR. 2003. New insights into grapevine flowering. Functional Plant Biology 30, 593–606.

Boss PK, Sreekantan L, Thomas MR. 2006. A grapevine TFL1 homologue can delay flowering and alter floral development when over expressed in heterologous species. Functional Plant Biology 33, 31–41.

Boss PK, Thomas MR. 2002. Association of dwarfism and floral induction with a grape 'green revolution' mutation. Nature 416, 847–850. Buban T, Faust M. 1982. Flower bud induction in apple trees: internal control and differentiation. Horticultural Reviews 4, 174– 203.

Bukovac MJ, Sabbatini P, Schwallier PG. 2006. Modifying alternate bearing of spur-type 'Delicious' apple with ethephon. HortScience 41, 1606–1611.

Buttrose MS. 1970. Fruitfulness in grape-vines: the response of different cultivars to light, temperature and daylength. Vitis 9, 121–125.

Buttrose MS, Alexander DM. 1978. Promotion of floral initiation in 'Fuerte' avocado by low temperature and short daylength. Scientia Horticulturae 8, 213–219. Cain JC. 1971. Effects of mechanical pruning of apple hedgerows with a slotting saw on light penetration and fruiting. Journal of the American Society for Horticultural Science 96, 664–667.

Chaikiattiyos S, Menzel CM, Rasmussen TS. 1994. Floral induction in tropical fruit trees: effects of temperature and water supply. Journal of Horticultural Science 69,

397–415.

Chan G, Cain JC. 1967. The effect of seed formation on subsequent flowering in apple. Proceedings of the American Society for Horticultural Science 91, 63–68.

Chen W. 1991. Changes in cytokinins before and during early flower bud differentiation in lychee (Litchi chinensis Sonn.). Plant Physiology 96, 1203–1206.

Chen WS. 1990. Endogenous growth substances in xylem and shoot tip diffusate of lychee in relation to flowering. HortScience 25, 314–315.

Corbesier L, Coupland G. 2005. Photoperiodic flowering of Arabidopsis: integrating genetic and physiological approaches to characterization of the floral stimulus. Plant, Cell and Environment 28, 54–66.

Corbesier L, Lejeune P, Bernier G. 1998. The role of carbohydrates in the induction of flowering in Arabidopsis thaliana: comparison between the wild type and a starchless mutant. Planta 206, 131–137.

Corbesier L, Vincent C, Seonghoe J, et al. 2007. FT protein movement contributes to long-distance signaling in floral induction of Arabidopsis. Science 316, 1030–1033.

Davenport T. 1990. Citrus flowering. Horticultural Reviews 12, 349–408. Davenport TL. 2000. Leaves are not necessary for citrus floral induction. Proceedings of the International Society of Citriculture IX Congress, 660–661.

Davenport TL. 2003. Management of flowering in three tropical and subtropical fruit tree species. HortScience 38, 1331–1335.

Davenport TL, Nunez-Elisea R. 1997. Reproductive physiology. In: Litz RE, ed. The mango: botany, production and uses. Wallingford: CAB International, 69–146.

Davenport TL, Ying ZT, Kulkarni V, White TL. 2006. Evidence for a translocatable florigenic promoter in mango. Scientia Horticulturae 110, 150–159.

Dennis FJ, Neilsen JC. 1999. Physiological factors affecting biennial bearing in tree

fruit: the role of seeds in apple. HortTechnology 9, 317–322.

Dorsey MJ. 1935. Nodal development of the peach shoot as related to fruit bud formation. Proceedings of the American Society for Horticultural Science 33, 245–257.

Eriksson S, Bohlenius H, Moritz T, Nilsson O. 2006. GA4 is the active gibberellin in the regulation of LEAFY transcription and Arabidopsis floral initiation. The Plant Cell 18, 2172–2181.

Faust M. 1989. Physiology of temperate zone fruit trees. New York: John Wiley & Sons. Forshey CG, Elfving DC. 1989. The relationship between vegetative growth and fruiting in apple trees. Horticultural Reviews 11, 229–287.

Foster T, Johnston R, Seleznyova A. 2003. A morphological and quantitative characterization of early floral development in apple (Malus3domestica Borkh.). Annals of Botany 92, 199–206.

Fulford RM. 1965. The morphogenesis of apple buds. I. The activity of the apical meristem. Annals of Botany 29, 167–182.

Fulford RM. 1966a. The morphogenesis of apple buds. III. The inception of flowers. Annals of Botany 30, 207–219.

Fulford RM. 1966b. The morphogenesis of apple buds. IV. The effect of fruit. Annals of Botany 30, 598–606.

Garcia-Luis A, Almela V, Monerri C, Agusti M, Guardiola JL. 1986. Inhibition of flowering in vivo by existing fruits and applied growth regulators in Citrus unshiu. Physiologia Plantarum 66, 515–520.

Garcia-Pallas I, Val J, Blanco A. 2001. The inhibition of flower bud differentiation in ‘Crimson Gold’ nectarine with GA(3) as an alternative to hand thinning. Scientia Horticulturae 90, 265–278.

Gazzani S, Gendall AR, Lister C, Dean C. 2003. Analysis of the molecular basis of flowering time variation in Arabidopsis accessions. Plant Physiology 132, 1107–1114.

Goldschmidt EE, Aschkenaki N, Herzano Y, Schaffer AA, Monselise SP. 1985. A role for carbohydrate levels in the control of flowering in citrus. Scientia Horticulturae 26, 159–166. Goldschmidt EE, Golomb A. 1982. The carbohydrate balance of alternate-bearing citrus trees and the significance of reserves for flowering and fruiting. Journal of the American Society for Horticultural Science 107, 206–208.

Grant JA, Ryugo K. 1984. Influence of within-canopy shading on fruit size shoot growth, and return bloom in kiwifruit. Journal of the American Society for Horticultural Science 109, 799–802.

Guimond CM, Andrews PK. 1998. Timing and severity of summer pruning affects flower initiation and shoot regrowth in sweet cherry. HortScience 33, 647–649.

Hackett WP, Hartmann HT. 1964. Inflorescence formation in olive as influenced by low temperature, photoperiod, and leaf area. Botanical Gazette 125, 65–72.

Harley CP, Magness JR, Masure MP, Fletcher LA, Degman ES. 1942. Investigations on the cause and control of biennial bearing of apple trees. United States Department of Agriculture Technical Bulletin 792.

Henriod RE, Jameson PE, Clemens J. 2003. Effect of irradiance during floral induction on floral initiation and subsequent development in buds of different size in Metrosideros excelsa (Myrtaceae). Journal of Horticultural Science and Biotechnology 78, 204–212.

Hirst PM, Ferree DC. 1995. Rootstock effects on the flowering of ‘Delicious’ apple. I. Bud development. Journal of the American Society for Horticultural Science 120, 1010–1017.

Hoad GV, Monselise SP. 1976. Effects of succinic acid 2, 2-dimethylhydrazide (SADH) on the gibberellin and abscisic acid levels in stem tips of M 26 apple rootstocks. Scientia Horticulturae 4, 41–47.

Ito A, Hayama H, Kashimura Y, Yoshioka H. 2001. Effect of maleic hydrazide on endogenous cytokinin contents in lateral buds, and its possible role in flower bud formation on the Japanese pear shoot. Scientia Horticulturae 87, 199–205.

Izawa T, Oikawa T, Sugiyama N, Tanisaka T, Yano M, Shimamoto K. 2008. Phytochrome mediates the external light signal to repress FT orthologs in photoperiodic flowering of rice. Genes and Development 16, 2006–2020.

Jackson DI. 1969. Effects of water, light and nutrition on flowerbud initiation in apricots. Australian Journal of Biological Science 22, 69–75.

Kinet JM. 1993. Environmental, chemical, and genetic control of flowering. Horticultural Reviews 15, 279–334.

King RW, Ben-Tal Y. 2001. A florigenic effect of sucrose in Fuchsia hybrida is blocked by gibberellin-induced assimilate competition. Plant Physiology 125, 488–496.

King RW, Moritz T, Evans LT, Martin J, Andersen CH, Blundell C, Kardailsky I, Chandler PM. 2006. Regulation of flowering in the long-day grass, Lolium temulentum L., by gibberellins and the gene FLOWERING LOCUS T (FT). Plant Physiology 141, 498–507. Koshita Y, Takahara T, Ogata T, Goto A. 1999. Involvement of endogenous plant hormones (IAA, ABA, GAs) in leaves and flower bud formation of satsuma mandarin (Citrus unshiu Marc.). Scientia Horticulturae 79, 185–194.

Kotoda N, Iwanami H, Takahashi S, Abe K. 2006. Antisense expression of MdTFL1,aTFL1-like gene, reduces the juvenile phase in apple. Journal of the American Society for Horticultural Science 131, 74–81.

Kotoda N, Wada M, Komori S, Kidou S, Abe K, Masuda T, Soejima J. 2000. Expression

pattern of homologues of floral meristem identity genes LFY and AP1 during flower development in apple. Journal of the American Society for Horticultural Science 125, 398–403.

Kotoda N, Wada M. 2005. MdTFL1,aTFL1-like gene of apple, retards the transition from vegetative to reproductive phase in transgenic Arabidopsis. Plant Science 168, 95–104. Kulkarni V. 1991. Physiology of flowering in mango studied by grafting. Acta Horticulturae 291, 95–104.

Kulkarni VJ. 1986. Graft-induced off-season flowering and fruiting in the mango (Mangifera indica L). Journal of Horticultural Science 61, 141–145.

Kulkarni VJ. 1988a. Chemical control of tree vigour and the promotion of flowering and fruiting in mango (Mangifera indica L.) using paclobutrazol. Journal of Horticultural Science 63, 557–566.

Kulkarni VJ. 1988b. Further studies on graft-induced off-season flowering and fruiting in mango (Mangifera indica L). Journal of Horticultural Science 63, 361–367.

Lakso AN. 1994. Apple. In: Schaffer B, Andersen PC, eds. Environmental physiology of fruit crops, Vol. 1. Boca Raton: CRC Press, 3–42.

Lavee S, Haskal A, Bental Y. 1983. Girdling olive trees, a partial solution to biennial bearing. I. Methods, timing and direct tree response. Journal of Horticultural Science 58, 209–218. Lenahan OM, Whiting MD, Elfving DC. 2006. Gibberellic acid inhibits floral bud induction and improves ‘Bing’ sweet cherry fruit quality. HortScience 41, 654–659.

Lifschitz E, Eshed Y. 2006. Universal florigenic signals triggered by FT homologues regulate growth and flowering cycles in perennial day-neutral tomato. Journal of Experimental Botany 57, 3405–3414.

Lin M-K, Belanger H, Lee Y-J, et al. 2007. FLOWERING LOCUS T protein may act as

the long-distance florigenic signal in the curcurbits. The Plant Cell 19, 1488–1506.

Lord EM, Eckard KJ. 1987. Shoot development in Citrus sinensis L. (Washington navel orange). II. Alteration of developmental fate of flowering shoots after GA3 treatment. Botanical Gazette 148, 17–22.

Luckwill LC. 1970. The control of growth and fruitfulness of apple trees. In: Luckwill LC, Cutting CV, eds. Physiology of tree crops. New York: Academic Press, 237–254.

Luckwill LC. 1974. A new look at the process of fruit bud formation in apple. XIX International Horticultural Congress Warszawa, Poland, 237–245.

Luckwill LC, Silva JM. 1979. The effects of daminozide and gibberellic acid on flower initiation, growth and fruiting of apple cv. Golden Delicious. Journal of Horticultural Science 54, 217–223.

McArtney SJ, Hoover EM, Hirst PM, Brooking IR. 2001. Seasonal variation in the onset and duration of flower development in 'Royal Gala' apple buds. Journal of Horticultural Science and Biotechnology 76, 536–540.

McLaughlin JM, Greene DW. 1984. Effects of BA, GA4+7, daminozide on fruit set, fruit quality, vegetative growth, flower initiation, and flower quality of 'Golden Delicious' apple. Journal of the American Society for Horticultural Science 109, 34–39.

Menzel CM, Olesen T, McConchie CA, Wiltshire N, Diczbalis Y. 2000. Lychee, longan and rambutan. Optimising canopy management. Canberra: Rural Industries Research and Development Corporation.

Menzel CM, Simpson DR. 1990. Effect of paclobutrazol on growth and flowering of lychee (Litchi chinensis). Australian Journal of Experimental Agriculture 30, 131–137.

Menzel CM, Simpson DR. 1987. Effect of cincturing on growth and flowering of lychee over several seasons in subtropical Queensland. Australian Journal of

Experimental Agriculture 27, 733–738.

Menzel CM, Rasmussen TS, Simpson DR. 1995. Carbohydrate reserves in lychee trees (Litchi chinensis Sonn.). Journal of Horticultural Science 70, 245–255.

Menzel CM, Simpson DR. 1995. Temperatures above 20 C reduce flowering in lychee (Litchi chinensis Sonn.). Journal of Horticultural Science 70, 981–987.

Michaels SD, Amasino RM. 1999. FLOWERING LOCUS C encodes a novel MADS domain protein that acts as a repressor of flowering. The Plant Cell 11, 949–956.

Moss GI. 1976. Temperature effects on flower initiation in sweet orange (Citrus sinensis). Australian Journal of Agricultural Research 27, 399–407.

Nagao MA, Ho-a EB, Yoshimoto JM. 1999. Uniconazole retards growth and increases flowering of young macadamia trees. HortScience 34, 104–105.

Nakata S. 1976. Progress report on flowering, nut setting and harvesting, with special reference to the effects of night temperatures and growth regulators. Proceedings of the Hawaiian Macadamia Producers' Association 16, 31–36.

Neilsen JC, Dennis FJ. 2000. Effects of seed number, fruit removal, bourse shoot length and crop density on flowering in 'Spenser Seedless' apple. Acta Horticulturae 527, 137–146. Nishikawa F, Endo T, Shimada T, Fujii H, Shimizu T, Omura M, Ikoma Y. 2007. Increased CiFT abundance in the stem correlates with floral induction by low temperature in Satsuma mandarin (Citrus unshiu Marc). Journal of Experimental Botany 58, 3915–3927.

Nunez-Elisea R, Davenport TL. 1994. Flowering of mango trees in containers as influenced by seasonal temperature and water stress. Scientia Horticulturae 58, 57–66.

Nunez-Elisea R, Davenport TL. 1995. Effect of leaf age, duration of cool temperature treatment, and photoperiod on bud dormancy release and floral initiation in mango.

Scientia Horticulturae 62, 63–73.

Nunez-Elisea R, Davenport TL. 1998. Gibberellin and temperature effects on dormancy release and shoot morphogenesis of mango (Mangifera indica L.). Scientia Horticulturae 77, 11–21. O'Hare TJ. 2004. Impact of root and shoot temperature on bud dormancy and floral induction in lychee (Litchi chinensis Sonn.). Scientia Horticulturae 99, 21–28.

Olesen T. 2005. The timing of flush development affects the flowering of avocado (Persea americana) and macadamia (Macadamia integrifolia3tetraphylla). Australian Journal of Agricultural Research 56, 723–729.

Olesen T, Menzel CM, Wiltshire N, McConchie CA. 2002. Flowering and shoot elongation of lychee in eastern Australia. Australian Journal of Agricultural Research 53, 977–983.

Pandey RM. 1989. Physiology of flowering in mango. Acta Horticulturae 231, 361–380.

Pena L, Martin-Trillo M, Juarez J, Pina JA, Navarro L, Martinez-Zapater JM. 2001. Constitutive expression of Arabidopsis LEAFY or APETALA1 genes in citrus reduces their generation time. Nature Biotechnology 19, 263–267.

Pillitteri LJ, Lovatt CJ, Walling LL. 2004a. Isolation and characterization of a TERMINAL FLOWER homolog and its correlation with juvenility in citrus. Plant Physiology 135, 1540–1551.

Pillitteri LJ, Lovatt CJ, Walling LL. 2004b. Isolation and characterization of LEAFY and APETALA1 homologues from Citrus sinensis L. Osbeck 'Washington'. Journal of the American Society for Horticultural Science 129, 846–856.

Pineiro M, Coupland G. 1998. The control of flowering time and floral identity in Arabidopsis. Plant Physiology 117, 1–8.

Rademacher W. 1995. Growth retardants: biochemical features and applications in horticulture. Acta Horticulturae 394, 57–73.

Ramirez H, Hoad GV. 1981. Effects of growth substances on fruitbud initiation in apple. Acta Horticulturae 120, 131–136.

Reece PC, Furr JR, Cooper WC. 1946. The inhibiting effect of the terminal bud on flower formation in the axillary buds of the Haden mango. American Journal of Botany 33, 209–210. Reece PC, Furr JR, Cooper WC. 1949. Further studies of floral induction in the Haden mango (Mangifera indica L.). American Journal of Botany 36, 734–740.

Reeves PH, Coupland G. 2001. Analysis of flowering time control in Arabidopsis by comparison of double and triple mutants. Plant Physiology 126, 1085–1091.

Rohde A, Bhalerao RP. 2007. Plant dormancy in the perennial context. Trends in Plant Science 12, 217–223.

Rohozinski J, Edwards GR, Hoskyns P. 1986. Effects of brief exposure to nitrogenous compounds on floral initiation in apple trees. Physiologie Ve´ge´tale 24, 673–677.

Salazar-Garcia S, Lovatt CJ. 1998. GA3 application alters flowering phenology of ‘Hass’ avocado. Journal of the American Society for Horticultural Science 123, 791–797.

Salomon E, Reuveni O. 1994. Effect of paclobutrazol treatment on the growth and first flowering of intact and autografted seedlings of mango. Scientia Horticulturae 60, 81–87. Searle I, He Y, Turck F, Vincent C, Fornara F, Krober S, Amasino RA, Coupland G. 2006. The transcription factor FLC confers a flowering response to vernalization by repressing meristem competence and systemic signalling in Arabidopsis. Genes and Development 20, 898–912.

Shu ZH, Sheen TF. 1987. Floral induction in axillary buds of mango (Mangifera indica L) as affected by temperature. Scientia Horticulturae 31, 81–87.

Simpson GG, Dean C. 2002. Arabidopsis, the rosetta stone of flowering time? Science 296, 285–289.

Singh LB. 1959. Movement of flowering substances in the mango (Mangifera indica L.) leaves. Horticultural Advances 3, 20–27.

Southwick SM, Davenport TL. 1986. Characterization of waterstress and low-temperature effects on flower induction in citrus. Plant Physiology 81, 26–29.

Spann TM, Williamson JG, Darnell RL. 2003. Photoperiodic effects on vegetative and reproductive growth of Vaccinium darrowi and V. corymbosum interspecific hybrids. HortScience 38, 192–195.

Spann TM, Williamson JG, Darnell RL. 2004. Photoperiod and temperature affects growth and carbohydrate storage in southern highbush blueberry interspecific hybrid. Journal of the American Society for Horticultural Science 129, 294–298.

Srinivasan C, Mullins MG. Effects of temperature and growth regulators on formation of anlagen, tendrils and inflorescences in Vitis vinifera L. Annals of Botany 45, 439–446.

Stern RA, Naor A, Wallach R, Bravdo B, Gazit S. 1998. Effect of fall irrigation level in ‘Mauritius’ and ‘Floridan’ lychee on soil and plant water status, flowering intensity, and yield. Journal of the American Society for Horticultural Science 123, 150–155.

Stutte GW, Martin GC. 1986. Effect of light intensity and carbohydrate reserves on flowering in olive. Journal of the American Society for Horticultural Science 111, 27–31.

Suarez-Lopez P, Wheatley K, Robson F, Onouchi H, Valverde F, Coupland G. 2001. CONSTANS mediates between the circadian clock and the control of flowering in

Arabidopsis. Nature 410, 1116–1120.

Sukhvibul N, Hetherington SE, Vithanage V, Whiley AW, Smith MK. 2000. Effect of temperature on inflorescence development and floral biology of mango (Mangifera indica L.). Acta Horticulturae 509, 601–607.

Sung SK, Yu GH, Nam J, Jeong DH, An G. 2000. Developmentally regulated expression of two MADS-box genes, MdMADS3 and MdMADS4, in morphogenesis of flower buds and fruit in apple. Planta 210, 519–528.

Takada S, Goto K. 2003. TERMINAL FLOWER2, an Arabidopsis homolog of HETEROCHROMATIN PROTEIN1, counteracts the activation of FLOWERING LOCUS T by CONSTANS in the vascular tissues of leaves to regulate flowering time. The Plant Cell 15, 2856–2865.

Tamaki S, Matsuo S, Wong HL, Yokoi S, Shimamoto K. 2007. Hd3a protein is a mobile flowering signal in rice. Science 316, 1033–1036.

Tongumpai P, Jutamanee K, Sethapakdi R, Subhadrabandhu S. 1991. Variation in level of gibberellin-like substances, during vegetative growth and flowering of mango cv. Khiew Sawoey. Acta Horticulturae 291, 105–107.

Trevaskis B, Bagnall DJ, Ellis MH, Peacock WJ, Dennis ES. 2003. MADS box genes control vernalization-induced flowering in cereals. Proceedings of the National Academy of Sciences, USA 100, 13099–13104.

Trevaskis B, Hemming MN, Peacock WJ, Dennis ES. 2006. HvVRN2 responds to daylength, whereas HvVRN1 is regulated by vernalization and developmental status. Plant Physiology 140, 1397–1405.

Trevaskis B, Hemming MN, Dennis ES, Peacock WJ. 2007. The molecular basis of vernalization-induced flowering in cereals. Trends in Plant Science 12, 352–357.

Tromp J. 1976. Flower-bud formation and shoot growth in apple as affected by

temperature. Scientia Horticulturae 5, 331–338.

Tromp J. 1980. Flower-bud formation in apple under various day and night temperature regimes. Scientia Horticulturae 13, 235–243.

Tromp J. 1982. Flower-bud formation in apple as affected by various gibberellins. Journal of Horticultural Science 57, 277– 282.

Tromp J. 2000. Flower-bud formation in pome fruits as affected by fruit thinning. Plant Growth Regulation 31, 27–34.

Turnbull CGN, Sinclair ER, Anderson KL, Nissen RJ, Shorter AJ, Lanham TE. 1999. Routes of ethephon uptake in pineapple (Ananas comosus) and reasons for failure of flower induction. Journal of Plant Growth Regulation 18, 145–152.

Turner A, Beales J, Faure S, Dunford RP, Laurie DA. 2005. The pseudo-response regulator Ppd-H1 provides adaptation to photoperiod in barley. Science 310, 1031–1034.

Valverde F, Mouradov A, Soppe W, Ravenscroft D, Samach A, Coupland G. 2004. Photoreceptor regulation of CONSTANS protein in photoperiodic flowering. Science 303, 1003–1006.

Wada M, Cao Q, Kotoda N, Soejima J, Masuda T. 2002. Apple has two orthologues of FLORICAULA/LEAFY involved in flowering. Plant Molecular Biology 49, 567–577.

Webster AD, Shepherd UM. 1984. The effects of summer shoot tipping and rootstock on the growth, floral bud production, yield and fruit quality of young sweet cherries. Journal of Horticultural Science 59, 175–182.

Weinbaum SA, DeJong TM, Maki J. 2001. Reassessment of seed influence on return bloom and fruit growth in ‘Bartlett’ pear. HortScience 36, 295–297.

Westwood MN. 1978 Flowering. In: Westwood MN (ed) Temperate-zone pomology. New York: Freeman. Whiley AW. 1993. Environmental effects on phenology and

physiology of mango: a review. Acta Horticulturae 341, 168–176.

Whiley AW, Rasmussen TS, Saranah JB, Wolstenholme BN. 1989. Effect of temperature on growth, dry matter production and starch accumulation in ten mango (Mangifera indica L.) cultivars. Journal of Horticultural Science 64, 753–765.

Wigge PA, Kim MC, Jaeger KE, Busch W, Schmid M, Lohmann JU, Weigal D. 2005. Integration of spatial and temporal information during floral induction in Arabidopsis. Science 309, 1056–1059.

Wilson RN, Heckman JW, Sommerville CR. 1992. Gibberellin is required for flowering in Arabidopsis thaliana under short days. Plant Physiology 100, 403–408.

Winston EC. 1992. Evaluation of paclobutrazol on growth, flowering and yield of mango cv. Kensington Pride. Australian Journal of Experimental Agriculture 32, 97–104.

Yan L, Loukoianov A, Blechl A, Tranquilli G, Ramakrishna W, SanMiguel P, Bennetzen JL, Echenique V, Dubcovsky J. 2004. The wheat VRN2 gene is a flowering repressor down-regulated by vernalization. Science 303, 1640–1644.

Yeshitela T, Robbertse PJ, Stassen PJC. 2004. Effects of various inductive periods and chemicals on flowering and vegetative growth of ‘Tommy Atkins’ and ‘Keitt’ mango (Mangifera indica) cultivars. New Zealand Journal of Horticultural Science 32, 209–215. Yeshitela T, Robbertse PJ, Stassen PJC. 2005. Effects of pruning on flowering, yield and fruit quality in mango (Mangifera indica). Australian Journal of Experimental Agriculture 45, 1325–1330.

Ying Z, Davenport TL. 2004. Leaves required for floral induction of lychee. Plant Growth Regulation Society of America Quarterly 32, 132–137.

Zhu LH, Borsboom O, Tromp J. 1997. Effect of temperature on flower-bud formation in apple including some morphological aspects. Scientia Horticulturae 70, 1–8.