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Flowering behaviors in annual and perennial fruit crops: A review

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Abstract
Flowering is a critical developmental transition in fruit crops that marks the switch from vegetative to reproductive growth of the plant. This transition period ultimately determines the yield potential, fruit quality, and orchard productivity of a crop. Annual fruit crops, such as strawberries, tomatoes, and cucurbits, can bear flowers rapidly after early vegetative growth, relying primarily on short-term environmental cues, including photoperiod, temperature, and nutrient status. In contrast, perennial fruit crops, such as mango, citrus, apple, and grape, follow multi-season flowering cycles regulated by dormancy release, carbohydrate accumulation, shoot maturity, and hormonal balance. Advances over the past two decades have highlighted the central role of FLOWERING LOCUS T (FT) genes, chilling-responsive dormancy-associated MADS-box (DAM) genes, stress-responsive pathways, and hormone interactions with carbohydrates in modulating floral induction across species. This review synthesizes recent knowledge on flowering physiology in annual and perennial fruit crops, emphasizing genetic, hormonal, environmental, and management-related factors that influence flower induction. Special focus is placed on short-day species, such as strawberry and tomatoes, stress-induced flowering in mango and citrus, dormancy-mediated induction in temperate fruits, and alternate bearing patterns. Understanding species-specific flowering controls is vital for improving climate resilience, adapting orchard management, and enhancing sustainable fruit production.

Keywords: Flower induction, annual fruit crops, perennial fruit crops, FT genes, dormancy, photoperiod, Hormonal regulation

1. Introduction

Flowering is a fundamental developmental milestone in fruit crops that determines the potential for fruit set and final yield. The transition from vegetative to reproductive growth is regulated by complex interactions between genetic pathways, environmental cues, and internal physiological statuses. In recent years, significant progress has been made in deciphering the flowering mechanisms of various horticultural crops. This has revealed conserved regulatory modules, such as CONSTANS (CO) and FLOWERING LOCUS T (FT) for photoperiod sensing, dormancy-associated MADS-box (DAM) genes for bud dormancy, and gibberellin and cytokinin antagonism for floral induction (Andres & Coupland, 2012; Falavigna *et al.* 2019) [2, 4]. Annual fruit crops, including tomatoes, cucurbits, and strawberries, complete their life cycle within a single season and typically flower shortly after attaining vegetative maturity. Their flowering behavior is strongly influenced by short-term environmental factors such as photoperiod, temperature, nutrient availability, and plant hormonal balance. Day-neutral and short-day flowering pathways dominate the regulation of flowering in these species. However, in perennial fruit crops, this contradicts the long lifespan and repeated cycles of vegetative and reproductive growth. Flowering regulation is more complex, as it involves processes such as winter chilling, carbohydrate storage, dormancy release, and shoot maturation. Flowering may initiate months before anthesis, as observed in apples, and grapes (Kurokura *et al.* 2013) [6]. Tropical and subtropical perennials, such as mango and citrus, rely heavily on cool temperatures, dry periods, and carbohydrate and hormone interactions to initiate flowering (Davenport, 2007; Agustí *et al.* 2022) [3, 1]. In recent years, climate variability has further complicated flowering patterns. Warmer winters, erratic rainfall, droughts, and shifting photoperiodic patterns have disrupted the normal floral induction cycles of several fruit crops. Consequently, understanding the underlying biological processes controlling flowering has become vital for

adapting orchard management, improving fruiting consistency, and strengthening resilience to climate change (Legave *et al.* 2015) [8].
This review comprehensively synthesizes the flowering mechanisms in annual and perennial fruit crops by integrating insights from molecular genetics, physiology, and environmental science. Special emphasis is placed on species-specific flowering behavior, hormonal regulation, alternate bearing, and crop management strategies.

2. Regulatory Mechanisms of Flowering in Fruit Crops: Flowering is a complex process governed by the interactions among genetic networks, environmental cues, and endogenous physiological factors. Recent research has significantly refined our understanding of these pathways, particularly the roles of photoperiod, temperature, drought stress, carbohydrate status, and hormones, in annual and perennial fruit crops.

2.1 Genetic Regulation of Flowering: Genetic control is intergrated with environmental signals and developmental cues to regulate floral induction. Several gene families play crucial roles in the successful flowering of various fruit crops. The CONSTANS (CO) transcription factor and its target, FLOWERING LOCUS T (FT), constitute the core photoperiodic flowering pathway. Long-day conditions activate CO, which induces FT expression in leaves. FT protein travels to the shoot apical meristem, triggering floral initiation (Andres & Coupland 2012) [2].

2.1.1 Annual Fruit Crops: In strawberries, the FT homolog FaFT1 activates flowering in short-day genotypes (Lei *et al.* 2015). However, in tomato, a day-neutral plant, FT-like genes such as SP5G (floral repressor) and SFT (floral activator) are utilized to regulate inflorescence development independent of day length.

2.1.2 Perennial Fruit Crops: Perennials have additional regulatory complexity because flowering must align with seasonal cycles. In apples, FT-like genes promote floral induction post-summer when environmental cues align with hormones (Mimida *et al.* 2013) [11]. In grapevines, the VvFT genes integrate temperature and light signals to regulate bud fruitfulness. In some perennial fruit crops in temperate climates, winter chilling is required to break endodormancy. The chilling-responsive DAM genes suppress flowering during dormancy, with high DAM expression suppressing floral induction and leading to dormant buds, whereas low DAM expression leads to floral induction DAM. gene functions have been validated in apples (Falavigna *et al.* 2019) [4]. This explains why insufficient winter chilling leads to poor bloom in apples which is a major concern for cultivation under warming climates (Heide *et al.* 2013) [5].

2.2 Stress-responsive Genetic Pathways: In tropical and subtropical perennials, such as mango and citrus, flowering is not governed by photoperiod or chilling. Instead, drought and cool temperatures regulate stress-responsive genes for flower induction. The pathways linking resource limitation and environmental stress to floral induction in these tropical and subtropical crops are mentioned below**.** Tropical fruit flowering, such as mango flowering, involves the activation of stress-related transcription factors, such as MiFT and MiSOC1, regulated by cool temperatures and carbon status (Ramirez and Davenport, 2010) [14]. Citrus utilizes the CiFT and CsAP1 pathways in response to drought-induced carbohydrate accumulation (Agusti, *et al.* 2022) [1].

2.3 Environmental Regulation of Flowering: Environmental cues are among the most critical regulators of fruit crops.

2.3.1 Photoperiod: Annual crops, such as strawberries, short-day cultivars, it flower under <14 hrs daylength and long-day types require >16 hrs (Heide *et al.* 2013) [5]. In perennial crops, the photoperiod plays a smaller role, especially in tropical perennials. Mango and citrus show weak photoperiodic regulation but respond mostly to temperature and drought fluctuations (Ramirez and Davenport, 2010; Mishra *et al.* 2024) [14, 12].

2.3.2 Temperature: Temperature regulates flowering in nearly all fruit crops. Low temperatures have a major influence on temperate fruits. It is essential for bud dormancy release in apples, insufficient chilling hours can lead to poor bloom, delayed flowering, and low fruit set (Heide *et al.* 2013) [5]. Moderate temperatures influence tomato and strawberry flowers at an average temperature of 20-25 °C. Generally, high temperatures (> 32 °C) delay flowering and promote abortion in tomatoes (Lee *et al.* 2023) [7].

2.3.3 Water Stress/Drought: Drought is a major flowering inducer in tropical perennials. In mango, cool and dry weather triggers shoot maturation and flowering. Drought stress enhances carbohydrate accumulation and activates the floral pathways (Davenport, 2007) [3]. In citrus, winter drought can enhance spring flowering by shifting carbohydrate partitioning to buds, and moderate water deficit can improve bud fruitfulness in some grape cultivars (Sodini *et al.* 2025) [17].

2.3.4 Light Intensity: Light quality and intensity have a significant influence on carbohydrate production, shoot vigor, and flower bud differentiation. In grapevines, high light exposure is required for fruitful buds and good cluster initiation (Sodini *et al.* 2025) [17]. Apple and pear buds exposed to shade show reduced flower initiation (Lee *et al.* 2023) [7].

2.4 Hormonal Regulation of Flowering: Endogenous hormones in plants interact to control floral induction in both annual and perennial fruit crops.

2.4.1 Gibberellins (GA): Gibberellins generally, inhibit flowering in many perennials, such as apple, citrus, and grape (Sodini *et al.* 2025) [17]. Excess GA promotes vegetative growth and reduces floral bud differentiation.

2.4.2 Cytokinins: Cytokinins promote cell division, carbohydrate transport, and floral bud initiation. The application of cytokinins increases flowering in grapes and apples by enhancing meristematic activity (Ramirez *et al.* 2004) [15].

2.4.3 Auxins: It regulate apical dominance and influence floral meristem identity. Auxin and cytokinin balance are crucial for flowering in tomatoe.

2.4.4 Abscisic Acid (ABA): It is important for stress-induced flowering in mango and citrus. It also regulates carbohydrate accumulation and drought responses in flower buds (Mishra *et al.* 2024) [12].

2.4.5 Ethylene: Ethylene promotes female flower formation in cucurbits. It also regulates floral organ development and sex expression (Li *et al.* 2019).

3. Flowering Behavior of Annual Fruit Crops

Annual fruit crops complete their life cycle within a single growing season and exhibit rapid flowering after vegetative growth. Unlike perennials, annuals do not undergo dormancy or chilling requirements and display higher phenotypic plasticity in their flowering response.

3.1 Strawberry (*Fragaria x ananassa*): Strawberries generally show a short-day photoperiodic requirement, but with recent advances, some day-neutral cultivars have also been found.

3.1.1 Short-day Strawberries: These cultivars initiate flowering when the day length is <14 hrs and temperatures are cool (10-18 °C). Under these conditions, flower buds differentiate rapidly (Heide *et al.* 2013) [5].

3.1.2 Day-neutral Strawberries: These flower continuously under a broad range of photoperiods, provided that the temperatures remain moderate (15-25 °C). They rely more on thermal time than on photoperiodic cues.

3.1.3 Physiology of Floral Induction: Low temperatures suppress vegetative stolon development and promote floral initiation in strawberries. Cytokinins and carbohydrate accumulation in the crown are key drivers of bud differentiation.

3.1.4 Genetic Basis: The flowering gene FaFT1 and its regulators mediate photoperiod responses, with FT-dependent and FT-independent pathways contributing to flowering, depending on the cultivar type (Lei *et al.* 2015).

3.2 Tomato (*Solanum lycopersicum* L.): Flowering behavior is heavily regulated by genetic, hormonal, and environmental factors. The florigenic protein SINGLE FLOWER TRUSS (SFT) and tomato ortholog of FT in Arabidopsis play a key role in this process. SFT is produced in mature leaves and transported to the shoot apical meristem (SAM), where it triggers a switch from vegetative to reproductive growth by activating floral initiation genes. A reduction in SFT levels can cause delayed flowering, fewer trusses, and poor fruiting. Although tomatoes are day-neutral, temperature and light quality influence flowering. The ideal temperatures (22-28 °C) and light rich in red wavelengths promote flowering, whereas extreme temperatures disrupt pollen development and can cause flower drop (Shalit *et al.* 2009) [16]. Hormones such as gibberellins stimulate floral initiation and anther development, auxin influence floral bud differentiation, and cytokinins promote meristem activity and inflorescence branching. The key regulatory balance between SFT and SELF-PRUNING (SP) determines whether the plant growth habit is determinate or indeterminate (Shalit *et al.* 2009) [16].

3.2.1 Genetic Basis of Flowering: SFT acts as a flowering signal produced in mature leaves that moves to the SAM to initiate flowering. Although several FT-like genes exist in tomatoes, SFT is the primary floral inducer. The interaction of SFT with other proteins and transcription factors regulates flowering time and inflorescence development.

3.2.2 Environmental Factors: Although tomatoes are day-neutral, they respond to temperature and light quality. Average temperatures between 22-28 °C during flowering promote uniform floral initiation, and red light enhances flowering through phytochrome activation. Exposure to extreme heat or cold disrupts pollen viability, leading to flower drop (Shalit *et al.* 2009) [16].

3.2.3 Hormonal Regulation: Hormones such as gibberellins stimulate flora initiation and anther development, whereas auxins influence floral organ differentiation. Cytokinins promote meristem activity and inflorescence branching in indeterminate cultivars. The SFT: SP antagonistic balance governs determinate versus indeterminate growth, impacting flowering and plant architecture.

4. Flowering Behavior of Major Perennial Fruit Crops:

Most perennial fruit crops display multi-seasonal flowering cycles regulated by dormancy, carbohydrate reserves, shoot maturity, hormonal balance, and environmental cues. Flowering may initiate several months before anthesis, particularly in temperate species, making precise regulation essential for orchard productivity.

4.1 Apple (*Malus domestica*): Flower bud initiation occurs in late summer of the previous season, whereas anthesis occurs in spring (Heide *et al.* 2013) [5]. Most temperate fruit crops require winter chilling to break endodormancy. Insufficient chilling hours lead to a reduction in flowering and fruit set.

4.1.2 Physiological Control: Carbohydrate accumulation in woody shoots and buds ensures sufficient energy for floral differentiation (Lee *et al.* 2023) [7]. Hormonal regulation involves low gibberellin levels, cytokinins that promote meristem activity, and ABA that mediates stress-induced floral readiness (Falavigna *et al.* 2019) [4].

4.1.3 Genetic Regulation: The DAM genes maintain dormancy in most temperate perennial fruits, and their downregulation after chilling triggers flowering in fruits (Falavigna *et al.* 2019) [4]. The FT homolog in apples (MdFT1) integrates environmental cues with floral initiation for successful flowering (Mimida *et al.* 2013) [11].

4.2 Mango (*Mangifera indica*): In mangoes, temperature drop and drought stress act synergistically to trigger floral induction (Ramirez & Davenport, 2010) [14]. Photoperiod has a minimal effect on flowering induction.

4.2.1 Physiological Regulation: Carbohydrate accumulation in mature shoots is essential for flower bud formation in mango. Hormonal balance greatly influences flowering, such as high gibberellin levels inhibiting flowering, while high levels of ABA and cytokinins promote bud differentiation in mango (Davenport, 2007) [3].

4.2.2 Alternate Bearing: Mango often exhibits alternate bearing. Heavy flowering one year (ON year) suppresses flowering in the next year (OFF year). The causes od alternate bearing include high GA levels from fruiting shoots and depletion of carbohydrate reserves, which leads to alternate bearing (Legave *et al.* 2015) [8].

4.3 Citrus (*Citrus spp.*): In citrus, mild winter drought enhances spring flowering by increasing ABA and carbohydrate availability in buds for flowering (Lee *et al.* 2023) [7]. Fluctuation in temperature and light availability also contribute, but photoperiod has minor influence in citrus flowering.

4.3.1 Hormonal Regulation: Hormones such as GA inhibit flowering, whereas ABA promotes stress-induced floral induction in citrus and cytokinins assist in floral meristem initiation in citrus (Mishra *et al.* 2024) [12].

4.4 Grapes (*Vitis vinifera*): The Floral primordia in grapes form in the previous season's growing stems. Hence, pruning plays a major role in determining which buds bear flowers, and it has been also observed that light exposure affects bud fertility in grapes (Sodini *et al.* 2025) [17].

4.4.1 Environmental and Physiological Regulation: Moderate water deficit and high light intensity improve bud fruitfulness in grapes. Hormonal balance also affects floral differentiation, with low GA, high cytokinins, and adequate ABA leads to better flowering.

4.5 Alternate Bearing in Perennial Crops: Alternate bearing is common in mango, citrus, and apple. This is caused by a heavy fruit load in one year, leading to the depletion of carbohydrates and suppression of flower induction in the next year (Legave *et al.* 2015) [8]. High GA levels in fruiting shoots inhibit bud differentiation. In some temperate crops, insufficient chilling or environmental stress can exacerbate irregular flowering in perennials (Heide *et al.* 2013) [5].

5. Management Practices to Improve Flowering: Optimizing flowering in fruit crops requires integrated approaches combining environmental management, hormonal treatments, nutrient management, and pruning techniques, with some species-specific strategies essential owing to differences between annual and perennial crops.

5.1 Strawberry: Strawberry flowering can be easily manipulated by photoperiod manipulation. Short-day cultivars flower under <14 hrs light. In contrast, day-neutral cultivars flower continuously under moderate temperatures (Heide *et al.* 2013) [5]. By providing adequate carbohydrate accumulation in the crowns to enhance bud differentiation and flowering.

5.2 Tomato: In tomatoes, moderate temperatures (20-25 °C) are maintained to prevent flower abortion. Ensuring balanced NPK nutrition to support shoot and inflorescence development and improve flowering.

5.3 Mango: We can induce uniform flowering in mangoes through controlled irrigation by withholding water for 2-3 weeks before the expected flowering season. The application of paclobutrazol suppresses excessive vegetative growth and enhances floral bud induction (Davenport, 2007) [3]. In addition, fruit thinning after heavy crops can minimize the alternate bearing habit of mango.

5.4 Citrus: Citrus flowering can be regulated by manipulating stress conditions. Mild water stress in winter helps stimulate flowering. Well-balanced nutrient management (boron and potassium) can also enhance flower bud differentiation and fruit set. Excessive vegetative growth should be avoided by pruning and canopy management to promote flowering (Mishra *et al.* 2024) [12].

5.5 Apple: In apples, MAD genes greatly influence flowering under climatic conditions. Ensuring adequate winter chilling for dormancy release can increase bud-flower differentiation. Pruning helps expose buds to light and maintain a carbohydrate balance for good flowering. To maintain hormonal balance, the application of cytokinins to enhance meristem activity in low-chill years can be beneficial for flowering in apples (Falavigna *et al.* 2019) [4].

5.6 Grapes: In Grapes, environmental stress, such as moderate deficit irrigation, improves bud fruitfulness. Canopy management can also ensure optimal light for bud differentiation and increase flowering in grapes. Hormonal treatments, such as GA3, may be used to balance vegetative growth and flowering.

5.8 Management to Reduce Alternate Bearing: Pruning is performed to balance the vegetative and reproductive growth of the crops, which helps in balancing the carbohydrate levels in plants. We can also reduce the crop load in ON years by fruit thinning. The application of chemicals, such as paclobutrazol, to mango trees reduces vegetative vigor and promotes floral induction (Davenport, 2007) [3]. A balanced nutrient supply, particularly boron and potassium, helps support bud differentiation and increase flower numbers (Mishra *et al.* 2024) [12].

6. Conclusion

Flowering behavior varies widely between annual and perennial fruit crops owing to differences in genetics, physiology, environmental sensitivity, and hormonal regulation. Annual crops (tomato, strawberry, and cucurbits) flower rapidly in response to short-term cues, such as photoperiod, temperature, and nutrient availability. In perennial crops (mango, citrus, apple, and grape), multi-seasonal signals, including dormancy release, carbohydrate reserves, shoot maturity, and environmental stress, are integrated for floral induction. Recent advances have highlighted the involvement of genetic mechanisms (CO-FT module, DAM genes), hormonal interactions (GA, cytokinins, auxins, ABA, and ethylene), and stress-responsive pathways in the regulation of flowering across species. Management practices, including photoperiod manipulation, water stress, pruning, nutrient optimization, and hormonal applications, can significantly improve flowering uniformity and productivity in both annual and perennial crops. Understanding these mechanisms is essential for enhancing fruit yield and quality, mitigating alternate bearing, adapting fruit crops to climate variability, and supporting sustainable horticultural practices.

Future research integrating molecular genetics, stress physiology, and precision horticulture will further refine flowering-control strategies, enabling more resilient and productive fruit crop systems.

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