



## Review

## Constraints to obtaining consistent annual yields in perennials. II: Environment and fruit load affect induction of flowering

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## ABSTRACT

In many commercial fruit crop species, high fruit load inhibits vegetative growth and floral induction. As a result, trees that had a high fruit load will bear few flowers and fruit the following year, along with abundant vegetative growth. We previously discussed how high fruit load interferes with concurrent shoot growth. Here we focus on how high fruit load impacts the process of flowering. Ascertaining the precise time at which specific buds begin the floral transition in each species is challenging. The use of indirect approaches to determine time of floral induction or evocation may lead to questionable conclusions. Annual and perennial plants appear to use conserved proteins for flowering induction and initiation. The accumulation or reduction of transcripts encoding proteins similar to *Arabidopsis* (annual) FLOWERING LOCUS T (FT) and TERMINAL FLOWER1 (TFL1), respectively, correlates well with flower induction in several diverse species. The recent use of such markers provides a means to formulate an accurate timeframe for floral induction in different species and holds promise in providing new insight into this important developmental event. A role for hormones in modulating the inhibitory effect of fruit load on floral induction is also discussed.

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### 1. Introduction

In many fleshy commercial fruit species, a biennial trend of fruit production is observed: high fruit load (ON) 1 year and low fruit load (OFF) the following year. This biennial mode of fruit production is termed “alternate bearing” [1–3]. Previously, we aimed to

**Abbreviations:** FT, FLOWERING LOCUS T; TF, transcription factor; FLC, FLOWERING LOCUS C; SOC1, SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1; TFL1, TERMINAL FLOWER 1; TIBA, 2,3,5-triiodobenzoic acid; QTL, quantitative trait loci.

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familiarize the reader with the main concepts of alternate bearing, as discussed by scientists from different fields [3]. We also focused on possible mechanisms by which high fruit load inhibits vegetative growth [3]. Without sufficient vegetative growth, few axillary buds (a source for inflorescences in many species) are formed. In addition, high fruit load reduces the potential of each bud to produce inflorescences [1,2]. This is the focus of the present review.

To understand how high fruit load interferes with the flowering process, one first needs to understand the mechanism that triggers flowering in each species [4]. We begin by defining the basic developmental events that lead to flowering. In some species, such as papaya and passion fruit [5], the meristem continuously initiates new flower primordia, similar to the previously discussed cucumber [3]. Flowers on these plants reach anthesis at different times of the year. Here we concentrate on species in which anthesis occurs once a year. In many of these perennials, anthesis occurs in the spring; however, the formation of flower primordia may occur ~9 months before anthesis in some species, and only weeks before anthesis in others. In those belonging to the latter group, flower formation is sometimes dependent on exposure to cold winter temperatures [4].

Although the growth habit of perennials is different from that of annuals, and there is large variation among the perennials, some of the key regulators of flower induction and initiation appear to be conserved, and to share similar functions, in both groups. We provide the uninitiated reader with a short summary of known molecular events that lead to flowering in model annuals, and review evidence that conserved proteins have similar roles in perennials. Expression of some flower-promoting genes appears to be up-regulated by cold winter temperatures in some species that require such temperatures for flowering, suggesting a possible point of intervention of the environment in the flowering process in those perennials.

We then discuss the evidence for fruit load affecting flower induction, and provide examples of past research attempting to identify the signals involved. In this context, we also review research on the role of internal plant hormones and reserves in either repressing or inducing flowering [6].

Finally, we summarize recent research which connects fruit load to expression of flowering genes. These results suggest that in some species, transcriptional regulation of FLOWERING LOCUS T (FT)-encoding genes is a point of integration of both positive (inductive environmental cues) and negative (high gibberellin or high fruit load) signals that modulate the extent of flower induction (Fig. 1).

## 2. Defining spatial and temporal events leading to anthesis

Researchers differ in their use of terminology to describe plant reproduction. To reduce ambiguity, we refer the reader to a glossary which provides our definitions of the terms that we use [3].

While flowers are formed by the shoot meristem, in many species, the first biochemical changes (including transcription/translation) to trigger flowering, termed ‘flower induction’, occur in the leaves. In such cases, both environmental and endogenous cues that inhibit or trigger flowering can be integrated by the leaves, affecting the degree of flower induction. For example, photoperiodic induction of flowering occurs in leaves that sense the change in day length and respond by producing a small mobile protein termed “florigen”, which is transported to the meristem via the phloem (see below). Events that occur in the shoot meristem, in response to flower induction but prior to flower initiation, are termed ‘floral evocation’ [7]. We use the term ‘flower initiation’ as the first morphological (microscopic) evidence of the production of flower primordia. Later on, these primordia differentiate into floral buds. Note that flower initiation often occurs months before anthesis.

While research in several model annual species has demonstrated that flower induction occurs in the leaves, in some cases, such as *Arabidopsis*, the same environmental cues also affect flowering genes directly in the meristem [8]. In *Pharbitis*, when environmental signals that inhibit flowering were provided specifically to the meristem, the plant did not flower, even when the leaves of the same plant were exposed to inductive environmental signals [9]. Thus, when looking at a variety of species and conditions, we observe evidence for flower induction in leaves, in leaves and meristems, and in some cases only in meristems.

Once the meristem becomes committed to forming flowers, inhibitors that act on stages before flower initiation are no longer effective. While there are examples of floral reversion [10] or flower abortion [5], in most cases, once flowers initiate they do not disappear, although many may not reach anthesis.

Some species, such as citrus, proceed rapidly from flower initiation to bud release, inflorescence elongation and anthesis. However, a long lag between floral initiation (summer) and anthesis (spring) occurs in other species, such as apples. The axillary flower buds enter a period of dormancy during this lag event.

In perennials, a subset of meristems needs to remain vegetative to sustain further growth cycles [11]. The identity (vegetative or reproductive) of the buds, is apparent after release, however the identity of the remaining dormant buds is, in many species, unclear without microscopic, biochemical or molecular evaluation or an event that triggers bud release. For example, pruning, fruit removal, better exposure to light, girdling, bending and hormone treatments can increase the percentage of released buds, many of which contain inflorescences [6,12].

Anthesis may last a week in some species, several months in others. Moreover, time to anthesis in flowers of the same cultivar may vary under different environmental conditions. Anthesis in the ‘Hass’ avocado cultivar takes 1–2 months in California, Israel and Chile, but lasts close to 8 months in the Michoacán region of Mexico, where avocado originated. Changes in patterns of anthesis can emanate from changes in timing of flower initiation or changes in the lag between initiation and anthesis. Determining the cause of these changes is important, because it helps clarify the time window during which external and internal cues may still influence events prior to flower initiation.

## 3. Proteins involved in floral induction, evocation and initiation

The functions of key proteins that control flowering seem to be conserved in annuals and perennials. Here we review the main findings in annuals and provide examples for similar roles in perennials. A few of the genes we mention have not been studied in perennials, and we name them as potential markers for further research.

In many annuals, environmental cues perceived by leaves promote a flowering response. Evidence for what could be a universal transmissible signal (termed florigen) that moves from induced leaves to meristems and triggers flowering, has been provided [reviewed in 13]. There is evidence that florigen is a protein, encoded by the *Arabidopsis* FT and TWIN SISTER of FT genes [reviewed in 14]. Both genes encode very similar proteins, and other plant genomes have genes encoding FT-like proteins. Genetic evidence indicates that these proteins promote flowering in many annual species [15–17].

Different species flower in different seasons, and flowering in each species may be triggered by different environmental cues. For example, in some plants flower induction is triggered by short photoperiods, in others by long photoperiods, and in yet others, flower induction is not affected by photoperiod [18]. Still,

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