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Review

Physiological and molecular basis of alternate bearing in perennial fruit crops

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ABSTRACT

In perennial fruit crops, reproductive success and productivity are principally governed by the core event, regular flowering. However, this feature bearing can be influenced by different factors *viz.* environmental conditions, germplasm, rootstocks, and cultural operations. The phenomenon of irregular bearing is more dominant in perennial fruit crops. In order to ensure regular and quality fruit production it is therefore, imperative to regulate the flowering phenology. The comparative studies conducted by the researchers for understanding the physiological and molecular aspects associated with regular and irregular bearing phenomenon in perennial fruit crops are helpful to understand the crux of flowering, discover the regulatory factors for regularity in bearing. Further, differential gene expression studies allow the identification of key genes related with the regular bearing feature. The identified candidate genes in this regard could be harnessed for selection of desirable parents, hybrids in early nursery stage, thus facilitating the plant breeders through precision breeding approaches. This paper reviews the current understanding of the physiological and molecular basis associated with the flowering phenology along with the impact of different factors on alternate bearing in perennial fruit crops.

1. Introduction

Globally, countries possess and maintain the genetic diversity of different fruit crops important to nutrition and health of mankind. However, their relative contribution to the total production has been decreasing. Different factors appear responsible for this trend decline *viz.*, dynamics of climate change, incidence of pests and diseases, lack of efficient rootstocks, irregular bearing etc., impacting sustainable livelihoods of growers through alternate bearing problem. Perennial fruit crops, in their phyto-gerantology, manifest two major multiannual reproductive strategies, 1) heavy fruit load ('On' crop) in one year, and 2) low fruit load ('Off' crop) in the following year. This phenomenon is prominently known as alternate bearing (AB) (Goldschmidt, 2013; Sharma et al., 2015). Some orange and grapefruit cultivars produce sufficient fruits in the first year, followed by a good amount of vegetative growth simultaneously. This results in profuse flowering during the following year also. Moreover, these crops possess efficient mechanism(s) to control the surplus fruit production. An index was given by Hoblyn et al. (1936) that estimated the intensity of deviation in yield during consecutive years. Then Wilcox (1944), named this index as the Biennial Bearing Index (BBI). The BBI has been widely used to study the tendency of fruit yields over orchards, individual trees, or branches (Wilcox, 1944; Jonkers, 1979). The BBI has been used in various fruit crops like in apple (Barritt et al., 1997), mango (Reddy et al., 2003), coffee (Cilas et al., 2011), citrus (Smith et al., 2004), pecan (Wood et al., 2004), and pistachio (Rosenstock et al., 2010). This index is calculated by dividing the sum of the individual tree yields to the differences in successive years. For an adult tree, generally three years are enough for the evaluation of the alternative bearing. If the index value is higher then it means higher alternation. However, Racsko

Abbreviations: ABI, alternate bearing index; ABA, abscisic acid; AFL2, apple floricula/lfy; AP, apetala; BBI, biennial bearing index; BFT, brothers of ft; CiFT, citrus flowering locus T; CO, constans; DEGs, differentially expressed genes; FI, flower induction; FLC, flowering locus c; FUL, fruitful; GAs, gibberellins; LFY, leafy; MABI, modified alternate bearing index; miRNA, micro RNA; SoC1, suppressor of over expression of constants; SPL5, squamosa promoter binding; SVP, short vegetative phase; TFL1, terminal flower1

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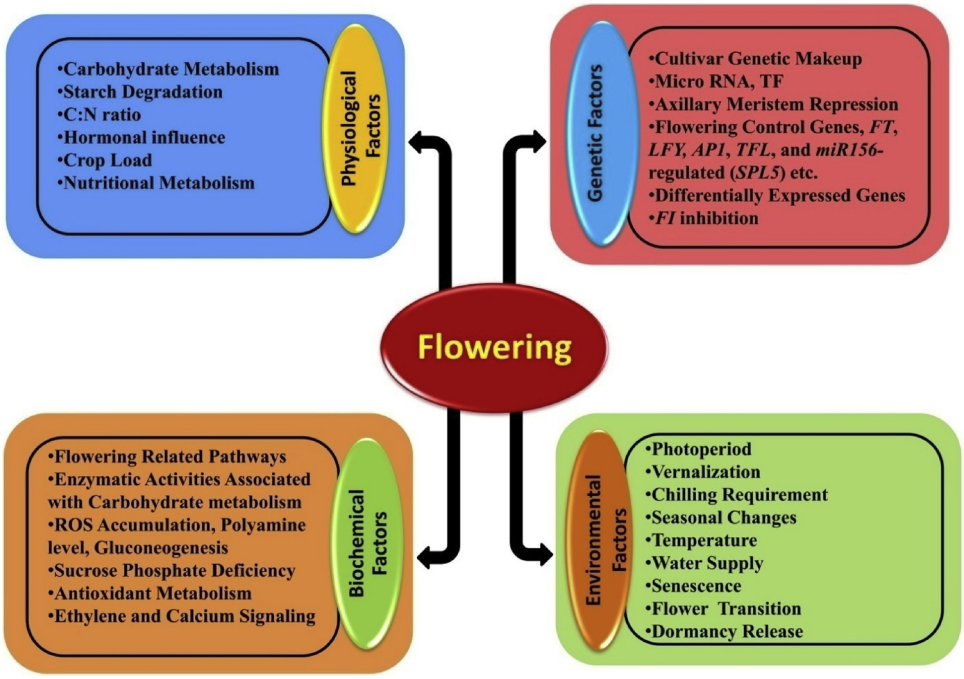

Fig. 1. Impact of various factors on bearing habit of perennial fruit crops.

(2008) reported that a fluctuation in yield is not sufficient for calculation of the alternate bearing. Then, researcher developed a new index so called “Modified Alternate Bearing Index” (MABI), which includes cultivar flower production to define alternate bearing. A significance test for biennial bearing was given by Huff (2001). Moreover, understanding the major events along with different environmental cues and molecular mechanisms that regulate the flower initiation, emerging of inflorescences, flower and fruit formation and effect of factors on existing fruit producing regions will be more useful (Khan et al., 2014). Extensive genomic and transcriptomic studies pave the way to discover the entire gene set, the subsets of genes mainly involved in the regulatory mechanism, various signal transduction systems, and the related metabolic pathways, focusing the identification of potential candidate genes to interpret the biological functions (Sharma et al., 2017).

2. Impact of different factors on alternate bearing

Flowering is governed either autonomously or by different external and internal factors and their interactions affect the flower formation in perennial fruit crops (Blázquez, 2000). Details of these factors are given in Fig. 1, Tables 1 and 2. For example, external factors like photoperiod, temperature, and water stress *etc.* and internal factors *viz.*: carbon-nitrogen ratio, hormones and interaction with other organs affect the flower formation in different fruit crops (Hanke et al., 2007; Bangerth, 2009; Takeno, 2016). For example flower set variability in apple due to the negative association between fruit development and flower bud differentiation (Foster et al., 2003) has been documented. Biennial bearing is also influenced by the number of seed per fruit or per bourse (Neilsen and Dennis, 2000). Mainly three important factors have been investigated for the alternate bearing phenomenon in perennial fruit crops (Goldschmidt, 2005). They include, i) reproductive and vegetative organs show the competition for the site of the flowering (Monselise and Goldschmidt, 1981); ii) differential amounts of nutrients during the ‘Off’ year (Rosecrance et al., 1998); and iii) endogenous phyto-hormonal control (Achard et al., 2006). Variable amounts of certain growth hormones in many fruit crops are considered core regulators for alternate bearing phenomenon (Baktir et al., 2004). Dag et al. (2010) showed that developing fruits appear to primarily depress vegetative growth and consequently the number of new and mature buds responsive to floral induction and floral initiation, so it seems to be the main factor governing the flowering and fruit yield in the following year in olive'. In light of the above, the foregoing explains how different factors affect the bearing tendencies in perennial fruit crops.

2.1. Cultivars/varieties

Cultivars within a given species vary in the bearing tendencies; some are regular bearers while others are alternate. For example, apple varieties show variable bearing tendencies with varieties like ‘Gala’, ‘Jonagold’, ‘Granny Smith’ and ‘Idared’ possess low alternate bearing index while, ‘Golden Delicious’ and ‘Fuji manifest’ high alternate bearing index. Haberman et al., 2016 have compared the regular and alternate (spur) type of Delicious varieties. Atay et al. (2013) studied the modified alternate bearing index (MABI) and classified the varieties into four relative classes. Varieties ‘Braeburn’ and ‘Jersey Mac’ come under no susceptible group; ‘Topaz’, ‘Granny Smith’, ‘Mondial Gala’, ‘Jonagold’, ‘Starkrimson Delicious’ and ‘Clear Red’ grouped into medium alternate whereas, ‘Kassel 37’, ‘Golden Reinders’ and ‘Kassel 41’ as showing highest level of alteration. The conceptual fact in this regard, is that varieties had the major impact on alternate bearing (Guitton et al., 2012; Smith and Samach, 2013). Earlier Crassweller et al. (2005) evaluated 20 apple varieties *viz.* ‘Arlet’, ‘Braeburn’, ‘Fuji’ and ‘Golden Delicious’ in order to know the extent of alternate bearing in the United States. Similarly, it was determined that variety ‘Golden Delicious’ and its strains had higher tendency to alternate bearing than the strains of ‘Delicious’. Spur-type Delicious cultivars such as ‘Starkrimson’ Delicious and ‘Red chief’ Delicious generally have alternate bearing behavior in respect of flowering and fruiting (Lauri et al., 2009).

Like apple, in mango research findings have clearly attributed this phenomenon to the varietal differences. Varieties with axillary fruit bearing habit possessed less alternate bearing tendencies than the terminal bearing ones. ‘Dashehari’, ‘Langra’ and ‘Chausa’ important choice cultivars of north India are alternate bearers. While south Indian varieties like ‘Totapuri Red Small’, ‘Bangalora’, and ‘Neelum’ are known to be regular bearers (Schnell and Knight, 1992). Response of mango varieties at different height of grafting on rootstock was studied by