

Impact of Rootstock *via* Carbohydrate Metabolism and Nutrients on Bearing Habit of Fruit Crops

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ABSTRACT

Fruits are widely regarded as protective food necessary for maintaining human health. Though growing fruit crops is a highly remunerative enterprise, their cultivation faces many challenges like fluctuations in climatic factors, irregular bearing, pests and diseases *etc.* This causes instability in production and productivity with low economic returns from per unit area. Alternate bearer fruit cultivars are one of the serious economic problems to the fruit growers. Physiological factors like carbohydrate reserves, nutrient metabolism and phytohormones are known to be involved in flowering thereby regulating bearing habit. Draining out of carbohydrate and nitrogen reserves during 'On' year is known to lead to a lean crop in the 'Off' year as they are important for fruit bud initiation *i.e.*, high C/N ratio helps for fruit bud initiation. The developing fruit provides a strong sink for photo assimilates. It was therefore, thought that depletion of photo assimilates, especially carbohydrates from the bud which prevents flowering induction, a hypothesis known as the nutritional theory. Knowledge about impact of carbohydrates and nutrients along with other important factors influencing flowering process is helpful in understanding the phenomena of bearing in fruit crops.

Keywords : Bearing habit, Carbohydrate metabolism, Fruit Crops, Nutrient uptake, Rootstock, Scion

FLOWER bud initiation is the key developmental stage in plant growth, particularly for horticultural crops such as the fruit trees because it determines the success of commercial orchards by its influence on fruit quantity and quality as well as stability of production from year to year. Fruit crops like mango, apple, citrus, litchi, olive *etc.* show irregular bearing. Improved technologies such as high-density planting, innovations in propagation, micro irrigation, protected cultivation, breeding for regular bearing, rootstock breeding for quality features and so on can help increase fruit yield. Fruit trees with various rootstock and scion combinations exhibit a variety of anatomical, physiological and biochemical characteristics. This will be helpful in understanding the impacts of the rootstock on different horticultural traits in fruit trees (Habibi *et al.*, 2022).

Major Research Gaps in Fruit Breeding for Regular Bearing

The instability in fruit production with good crop during one year and low or no crop in the following year is called as alternate bearing. Commonly used terms related to alternate bearing include biennial bearing and irregular bearing. Monselise and Goldschmidt (1982) reported that this phenomenon is present in many fruit tree crops, *viz.*, nuts (hazelnuts, pecans, pistachios and walnuts), temperate fruits (apple, apricot, pears and prunes), subtropical fruits (avocados, citrus and olives), tropical fruits (litchi and mango). Over the previous few years, India's horticulture production has increased. During last decade, area under horticulture grew by 2.6 per cent per annum with 4.8 per cent increase in production

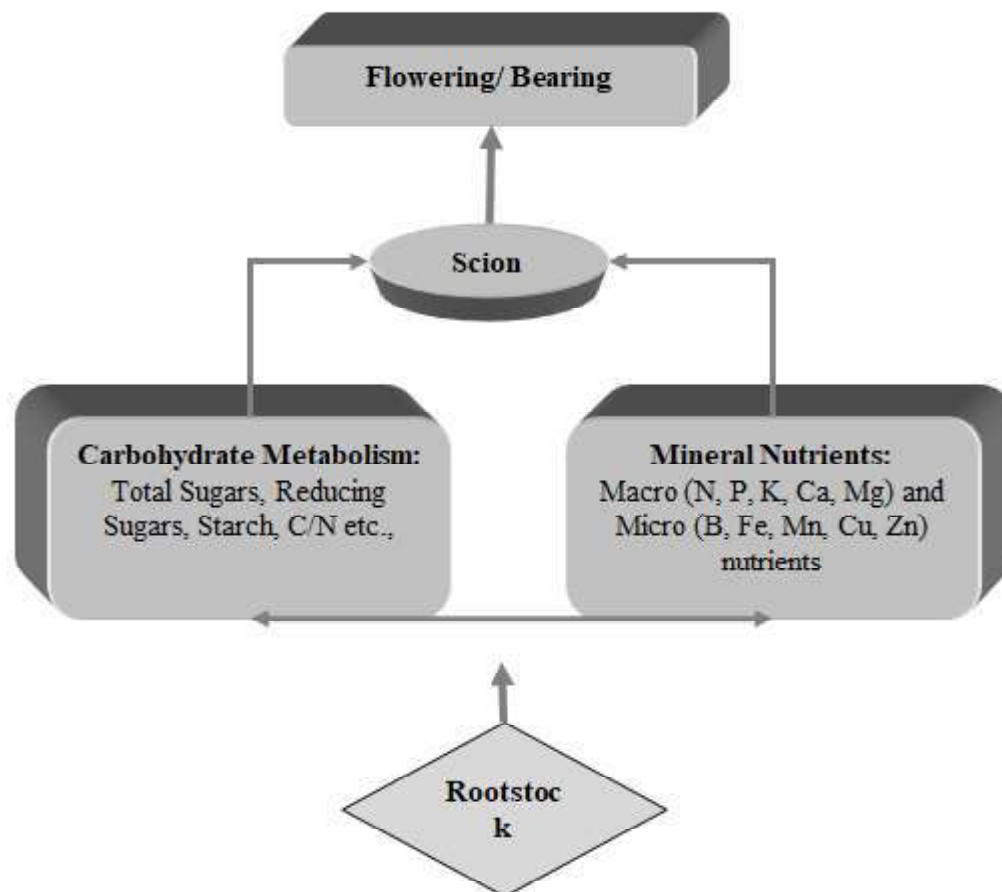


Fig. 1 : Rootstock influence on flowering or bearing habit of fruit crops *via* CHO metabolism and mineral nutrients.

(NHB, 2020-2021). However, variable fruit yield throughout subsequent years is a serious issue that restricts fruit crop productivity. Due to long juvenile phase, heterozygous in nature, breeding methods applicability for regular bearing is very cumbersome. Research on perennial crops for regular bearing has been carried out by several workers (Sharma *et al.*, 2019). There are many factors to regulate bearing of crop and carbohydrate metabolism and nutrient uptake also play an important role in bearing of crop. Role of rootstock for regular bearing is still meager therefore; present review highlights the role of rootstock in bearing.

Impact of Rootstocks on Physiological Traits of Fruit Crops

Numerous studies (Goncalves *et al.*, 2003 and Hartmann *et al.*, 2011) have shown that scion-

rootstock interactions influence the physiological traits of plants like photosynthetic variables (stomatal conductance, rate of transpiration, net rate of photosynthesis), water relations, anti-oxidant enzyme activities, total soluble protein (TSP) concentrations, mineral uptake, plant size, flowering, timing of fruit set, fruit quality and yield efficiency.

In grape, cherry and apple, genotypic effect of the rootstocks has altered the photosynthesis of the scion (Verma *et al.*, 2010). Satisha *et al.* (2007); Singh and Rajan (2009); Koepke and Dhingra (2013); Bavaresco and Lovisolo (2015) found that water use efficiency (WUE), photosynthesis variables *etc.* significantly differed among rootstocks and stress levels in fruit crops. Several studies (Loreti *et al.*, 2002; Haak *et al.*, 2006; Sotiropoulos, 2006; Bosa *et al.*, 2014) on pear and quince rootstocks indicated that scion-rootstock interactions have an impact on gas exchange, tree vigour, fruit set, yield and fruit quality.

Rootstock Influence on Flowering via CHO Metabolism

Effect of Rootstock on Carbohydrate Partitioning

Carbon and Nitrogen are the key elements because it is an energy-producing factor and build tissues, respectively. The importance of the Nitrogen Carbon (NC) ratio in flowering concept has been known since 1918. It was documented by the work of Kraus and Kraybill. Foster *et al.* (2017) studied that rootstock affects the partitioning of carbohydrates on both sides of the graft union in apple. Shu *et al.* (2017); Wang *et al.* (2016) found that plant growth regulators, proteins, mineral nutrients and water, are exchanged between the scion and root stock. Dayal *et al.* (2017) assessed the potential role of polyembryonic rootstocks on tree growth, yield and physiology of five mango cultivars. It is concluded that rootstocks alter most of the physio-chemical parameters of scion cultivars in mango though the extent of regulation of activities was scion specific.

In mango several studies (Reddy *et al.*, 2003; Smith *et al.*, 2003) found that the use of rootstocks has improved the growth, yield and fruit quality of mango. Costes *et al.* (2003); Costes and García-Villanueva, (2007) found that in fruit crops, like apple, rootstock impacts on scion growth habits which can affect the balance between reproductive and vegetative growth. Jover *et al.* (2012) observed that sucrose and starch concentrations in root bark appeared to be related with fruit sink strength. The phloem is main channel in supply of carbohydrates to developing plant tissues, including the flower (Boldingh *et al.*, 2016).

Yang *et al.* (2021) hypothesized that crop load manipulation has long been used to alter source - sink relationship to improve fruit quality and mitigate biennial bearing in fruit crops. Kviklys and Samuoliene (2020) reported that return to bloom was dependent on rootstock, scion and crop load and was negatively correlated to sorbitol in the buds. Abdullah *et al.* (2020) concluded that mango rootstock can affect canopy architecture of scion as early as in

the first year of growth following grafting. Fu *et al.* (2016) showed that grafting was associated with significantly increased plant growth, fruit yields and enhanced photosynthetic capacities in melon (*Cucumis melo*).

Importance of CHO Metabolism in Flowering / Fruiting

Experimental evidence indicates that maturity of terminal shoot and accumulation of carbohydrate in the leaves and shoot apex are in some way associated with the synthesis of the floral stimulus in mango trees (Davenport, 2009). Nath and Singh, (2014) suggested that carbohydrate distribution pattern may serve as an indication for the judging of the floral induction effect in litchi. Barbier *et al.* (2015) investigated how sugar availability modulates the hormonal network during bud outgrowth in Rosa hybrid. Upreti *et al.* (2014) studied the role of carbohydrates in the paclobutrazol induced floral initiation in mango cv. Totapuri. The results indicated that paclobutrazol induced flowering is accompanied by an increase in starch in leaf concomitant with an increase in soluble sugars in the apical buds. Maurel *et al.* (2004) found that vegetative buds of peach (*Prunus persica* L. Batsch.) trees act as strong sinks and their bud break capacity can be profoundly affected by carbohydrate availability during the rest period (November-February). Boldingh (2016) reported that high carbohydrate and boron content in flowers of avocado at anthesis must for fruit setting. Iglesias *et al.* (2002) generated source - sink imbalances by defoliation and sucrose supplementation by stem injection in cv. Okitsu of Satsuma mandarins and reported that sucrose supplementation increased citrus fruit set by more than 10 per cent.

Syvertsen *et al.* (2003) showed that leaves immediately adjacent to fruit were smaller, had lower leaf nitrogen and carbohydrate concentrations, lower leaf dry mass per area (LDM_a) and lower net assimilation of CO₂ (A_n) than leaves on non-fruiting branches of the same trees in 'Spring' navel Orange (*Citrus sinensis* (L.) Osbeck). Carbohydrate partitioning also play important role in alternate bearing. Davie *et al.* (1995) emphasized that

carbohydrate reserve must be increased in the tree at the flower induction to fruit set stage to modify the alternate bearing. Further, Jyothi *et al.* (1998) studied the biochemical changes in alternate and regular bearing varieties. In regular bearing trees, reducing sugars were highest at flower bud differentiation (FBD). Non-reducing and total sugar levels rise and fall pattern was noted from FBD to maturity.

Slow mobilization of starch reserves may be one limiting factor in citrus. Ulger *et al.* (2004) in their studies found a higher C/N ratio (1.5 times more in 'Off' than 'On' year) during the initiation period and an increased yield in the following year, suggest that sugar levels are associated with floral initiation in olives. Gawankar *et al.* (2019) studied that growth and fruitfulness of a plant is greatly influenced by the relative proportions of carbohydrates and nitrogen. Muñoz-Fambuena *et al.* (2013) did the proteomic analysis of leaves and floral buds from 'On' and 'Off' trees at the time of floral induction in citrus showed the importance of C and N compounds for flowering.

Saxena *et al.* (2014) showed that Amrapali being the regular cultivar, contained higher levels of total and reducing sugar and protein content in all the developmental stages of flowering as compared to biennial cultivars. The forms of sugar, as well as the ratio of reducing to non-reducing sugar and the total sugars, have a significant impact on fruit bud differentiation. Das *et al.* (2019) in their experiment analyzed the carbohydrate levels during flowering in two mango cultivars, Amrapali (regular bearer) and Dashehari (alternate bearer), contrasting for bearing habit. Regular bearer cv. Amrapali has a higher carbohydrate content than alternate bearer Dashehari during the 'Off' year. Capelli *et al.* (2021) investigated the role of hormones and carbohydrates on the negative effects of reproduction on vegetative growth in mango cultivars. Singh and Sharma, (2008) observed that physiological and biochemical changes associated with the flowering in mango. Shivashankara & Mathai, (2000); Urban *et al.* (2008) suggested that the changes in photosynthetic rate associated with flowering are reversible, it is associated with carbohydrate reserves accumulation

in reproductive shoot. Vemmos, (2005) reported that reduction in sucrose movement from leaves to inflorescent buds inhibits bud growth and triggers inflorescent bud abscission in pistachio (*Pistacia vera* L.). Goetz *et al.* (2021) showed that during the end of flowering transition, dominance inhibition of inflorescence shoot growth by fruit load is mediated by auxin and sugar signaling in Arabidopsis. Martínez-Alcántara *et al.* (2015) concluded that carbon utilization by fruit limits shoot growth in alternate-bearing citrus tree. In star fruit (*Averrhoa carambola*) drought stress increased the flowering rate in both drooping and water shoots (Pingping *et al.*, 2017). Stress caused increased accumulation of carbohydrates which may related to flowering.

Rootstocks-CHOs-Alternate Bearing

Fruiting depletes the carbohydrate supply, which is one of the most essential factors for biennial bearing in perennial fruit crops and is connected with floral induction. Diversion of assimilates from shoot apices to floral primordial is required for floral initiation. Off-season, summer flowering and winter fruiting was induced in mango cvs. Dashehari and Totapuri, which normally do not flower out of season, when their defoliated shoots were grafted onto the shoots of the off-season cv Royal Special. Off-season flowering could be readily induced in single flowering cultivars such as Alphonso and Dashehari by veneer grafting their defoliated receptor shoots onto leafy donor shoots of multi-flowering cultivars such as Royal Special (Kulkarni, 1986).

Some rootstocks can affect flowering time by altering the chilling requirement and lead to flowers opening (Atkinson and Else, 2001). Furthermore, the rootstock can influence the alteration of vegetative shoots to flowering buds (Seleznyova *et al.*, 2008). In addition, rootstocks determine the number of flowers on a tree caused by changes in scion architecture, shoot growth, and orientation (Van Hooijdonk *et al.*, 2011). Fruit rootstocks can induce precocious scion flowering. Rootstocks might affect alternate bearing through physiological factors favouring production, such as the amount of photosynthate translocated into parts of the roots (Kriedemann, 1969). Dwarf apple

rootstocks affect precocity and flowering time due to carbohydrate metabolism and enhanced carbon partitioning to the reproductive areas (Fazio *et al.*, 2014). Dubey *et al.* (2021) observed that rootstock influenced the vigour of scion and yield, but minimal alterations in fruit quality. Cohen *et al.*, (2022) reported that for vegetative rootstocks alternate bearing index (ABI) values were lower than the seedling rootstocks in avocado.

Rootstock Influence on Flowering via Nutrient Metabolism

Effect of Rootstock on Mineral Nutrient Uptake

Several reports (Cheng and Raba, 2009; North and Cook, 2006), showed that rootstocks can affect the mineral uptake of tree. According to several research, rootstock selection can have a considerable impact on nutrient uptake (Ibacache and Sierra, 2009; Covarrubias *et al.*, 2016; Habran *et al.*, 2016; Lecourt *et al.*, 2015; Zamboni *et al.*, 2016). Mickelbart *et al.* (2007) studied nutrient concentrations in ‘Hass’ avocado (*Persea americana* Mill.). In addition, citrus rootstocks affected boron uptake (Guidong *et al.*, 2011; Liu *et al.*, 2013; Mei *et al.*, 2011; Wang *et al.*, 2016). Rootstocks can affect mineral uptake, transport, and use efficiency from the soil through the root to the scion (Amiri *et al.*, 2014; Nawaz *et al.*, 2016). These attributes may be due to root architecture, changing the activities of ion transporters, changes in hormonal levels and miRNAs (Meister *et al.*, 2014; Zeng *et al.*, 2014).

The different architectures of grapevine rootstocks affected nitrogen use efficiency (NUE) and Phosphorus (P) uptake. The total nitrogen accumulation and NUE were affected in various citrus rootstocks, as rough lemon had more potential of NUE than ‘Cleopatra’ mandarin (Sorgona *et al.*, 2006). Prunus rootstocks significantly affected macro and microelements in leaves of cherry (Hrotko *et al.*, 2014), peach (Mestre *et al.*, 2015; Zarrouk *et al.*, 2005) and plum (Reig *et al.*, 2018), as well as flowers in cherry (Jiménez *et al.*, 2004) and peach (Zarrouk *et al.*, 2005). Consequently, rootstock modifies the transport of nutrients. For example, eight distinct K

transporters have been found in ‘Carrizo citrange’ and ‘Cleopatra’ mandarins (Caballero *et al.*, 2013). The activities of ferric-related uptake and transport genes (NAS1, FRD3 and NRMAP3) significantly increased ferrous uptake in apple rootstocks under iron-deficient conditions (Zha *et al.*, 2014). Two Prunus rootstocks showed increased expression of Ferric chelate reductase (FCR) and the iron transporter genes grown under iron-deficient conditions (Gonzalo *et al.*, 2011). Different grape rootstocks improved nitrate uptake by affecting the activities of low and high-affinity nitrate transporter genes (Tomasi *et al.*, 2015). In pear rootstocks, transcripts of ammonium transporters have been found to be affected by the rootstock (Li *et al.*, 2016; Mota *et al.*, 2007). Nitrogen uptake and transport in two graft combinations of grapevine, conferring different vigour to the scion. The low vigour rootstock had higher nitrate uptake capacity and assimilation in roots after nitrate resupply than the high vigour rootstock, which is potentially linked to the higher carbohydrate status of the low vigour rootstock. Sarkhosh *et al.* (2021) investigated the effect of rootstock on scion nutritional status and the selection of rootstock-scion combinations for variety development.

Importance of Mineral Nutrients in Flowering/Fruiting

Role of nutrients in irregular bearing also studied in many fruit crops. Nafees *et al.* (2013); El-Motaium *et al.* (2019) recommended nitrogen fertilizer to mitigate alternate bearing in mango. Fernandez-Escobar *et al.* (1999); Turktas *et al.* (2013), studied mineral nutrients in olive leaves during the alternate-bearing cycle. It was concluded that alternate bearing influenced leaf-nutrient content of olive trees. Pillay *et al.* (2005) observed that lower levels of leaf boron could help identify an ‘Off’ tree. Thus, signified the role of mineral elements in regulating the flowering. Baninasab *et al.* (2007) demonstrated that N, P and K concentrations were significantly lower in many organs of ‘On’ trees (presenting major bud abscission) than of ‘Off’ trees of Pistachio. Okada (2004); Mirsoleimani *et al.* (2014) showed that reserved nutrients status in citrus can predict the fruit

productivity. Gundesli *et al.* (2021) studied the seasonal changes in mineral nutrient contents in the leaf and shoot tissues of pistachio trees as well as the relationship between these changes and alternate bearing.

There is some evidence of an interrelationship between transport and metabolism of carbohydrates as well as movement and accumulation of K. It is well established that K acts as an osmoticum for the transport and storage of sugars (Giaquinta *et al.*, 1983). Thus, in 'On' trees there would be an enhanced requirement for K as an osmoticum for the transport of sucrose to the developing fruits. Krishnamurthy *et al.* (2013) investigated the influence of carbohydrates, mineral nutrients and plant hormones in alternate bearing of Black Pepper (*Piper nigrum* L.) and their study indicated that efficient utilization of metabolites in 'On' year may render vine weak in the subsequent year coupled with poor remobilization into developing berries, which could make it an 'Off' year. Physiological and biochemical attributes that help the rootstocks to control plant vigour have generally focused on hormone biosynthesis, nutrient uptake (Khan *et al.*, 2020), carbohydrates (Gemma and Iwahori, 1998).

Molecular Aspects: Bearing

The transport of molecules, mainly miRNA, small RNA and proteins across graft union through the phloem are important communication between rootstock and scion (Harada, 2010; Pant *et al.*, 2008; Xing *et al.*, 2016). The long-distance of mRNA, small RNA and protein as graft-transmissible signals are currently developing as new mechanisms to influence horticultural attributes in rootstock / scion relationships and play a crucial function in molecular aspects of grafting (Loupit and Cookson, 2020). Guo *et al.*, 2021 did fruit transcriptomics analysis revealed important differences in gene expression between pumpkin-grafted and self-grafted watermelon plants, highlighting a particular impact in ABA-signaling, sucrose transport and carotenoid metabolism related genes associated to the ripening process affected by the pumpkin rootstock.

Goncalves *et al.*, 2019 recommended that the rootstock was responsible for inducing the drought tolerance in scion cultivar by up regulating the transcription of genes associated to the cell wall, biotic as well as abiotic stress resistance, antioxidant systems, soluble carbohydrate, transcription factors (TFs), protein kinases (PKs) and proteins involved in the abscisic acid (ABA) signaling pathway and at the same time by down regulating the activity of genes involved in the light reaction, metabolic processes and biosynthesis of ethylene. Li *et al.* (2003) found that gene expression is related to starch accumulation in all 'Off' tree organs. RNA levels of all the genes examined were high in leaves and bark that accumulated high concentrations of starch and low in roots with declining starch concentrations. Yanik *et al.* (2013) performed a comprehensive study on the olive tree miRNA related to the alternate bearing. Wahl *et al.* (2013) studied the role of carbohydrates especially Trehalose-6-Phosphate in flowering of *Arabidopsis thaliana*. The loss of *TREHALOSE-6-PHOSPHATE SYNTHASE 1 (TPS1)* causes *Arabidopsis thaliana* to flower extremely late. This suggests that TPS1 is required for the timely initiation of flowering. It was concluded that the T6P pathway affects flowering both in the leaves and at the shoot meristem. Nebauer *et al.* (2014) carried out an experiment to find the relation between the seasonal variation of expression and activity of the genes involved in carbon metabolism and the partition and allocation of carbohydrates in 'Salustiana' sweet orange trees with different crop loads. Sharma *et al.* (2020) studied the molecular mechanisms underlying alternate bearing in mango (*Mangifera indica* L.) via transcriptome wide gene expression profiling of both regular and irregular mango varieties. Gould *et al.* (2019) showed differences in sugar delivery rate to the flower reflected by differences in *TPS1* expression. Yang *et al.* (2014) showed that mature leaves had higher expression levels of the floral promoter and florigen in litchi. The enzymes like Sucrose 6 Phosphate Synthase, Trehalose Phosphate Synthase, Citrate Synthase, Alcohol Dehydrogenase involved in the process of carbohydrate metabolism of plants (Brownleader *et al.*, 1997). Micallef *et al.* (1995)

reported the involvement of *Sucrose Phosphate Synthase (SPS)* gene in flowering of transgenic tomato. Role of *Citrate synthase (CS)* gene in flowering of transgenic tobacco and transgenic Arabidopsis plants (Han *et al.* 2013, 2017) was reported. Studies (Eldik *et al.*, 1998 and Gregerson *et al.*, 1991) indicated the involvement of Alcohol dehydrogenase activity in flowering. In plants grown under normal, aerobic conditions, *adh* genes are only transcribed in the anther, whereas ADH enzyme activity is localized in the pollen.

Effective Nutrition Regulation to Mitigate Irregular Bearing

The efficient utilization of metabolites and nutrients in on year may render the shoot week in the subsequent year coupled with poor remobilization into developing fruits, which could make it an 'Off' year.

The nutrients level during critical stages of plant growth plays an important role in production. Therefore, maintaining optimum nutrient balance in plant is essential. Appropriate levels of N, P, K, Mg, S and micronutrients were found necessary along with proper balance of Ca and other cations for flowering and fruit bearing.

The seasonal pattern of nutrient uptake and partitioning is a key component of fertilizer management in orchards. Matching both the time and the rates of fertilizer application with the time of a plant's high nutrient demand, not only maximizes yield, but also increases nutrient-use efficiency and thus, reduces the potential for pollution.

The nutrient management during 'Off' year to obtain higher yields and measures to achieve higher remobilization into developing fruits and enhancement of hormone levels through exogenous supplement during flower primordial initiation and early flowering stages during 'Off' year are helpful to counter the alternate bearing effect.

Conclusion and Future Thrust

Fruit removal studies have shown that flowering and fruiting are high energy requiring processes and

deplete high amounts of stored carbohydrates, nitrogen reserves as well as other mineral nutrients from previous season and there are no reserves to support the next year crop. This knowledge about impact of carbohydrates and nutrients along with other important factors influencing flowering processes helpful in understanding the phenomena of bearing in fruit crops and to take proper actions which will be helpful in reducing the impact of irregular bearing on productivity of fruit crops.

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