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Alternate bearing and the possible role of carbohydrates in bud abscission of pistachio (*Pistacia vera* L.)

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Abstract. Pistachio produces an abundant number of inflorescent buds every year (during spring and early summer) which abscise mainly on fruiting branches during seed development. Competition of the developing ovaries/seeds with inflorescent buds for nutrients was suggested as being primarily responsible for bud abscission. Although leaf N correlated with bud retention, foliar application of N did not reduce bud drop. Inflorescent buds on defruited branches accumulated twice as much ¹⁴C-photosynthate as those on fruiting ones. A depletion of carbohydrates in flower buds in "on" year trees was found by some researchers during seed development. Sucrose movement from leaves to flower buds was also reduced, resulting in a decrease of flower bud development on the "on" year trees which was followed by abscission. The possibility that depletion of carbohydrate in several organs of "on" trees during seed development triggers bud abscission resulting in alternate bearing is reviewed.

Keywords. Pistachio – Alternate bearing – Bud abscission – Nutrients – Carbohydrates – Hormones.

L'alternance de production fruitière et le rôle possible des hydrates de carbone dans l'abscission du pistachier (*Pistacia vera* L.)

Résumé. Le Pistachier produit un nombre abondant de bourgeons floraux chaque année (pendant le printemps et le début de l'été) qui subissent une abscission principalement sur les branches fruitières pendant le développement des graines. La concurrence pour les éléments nutritifs, des ovaires/des graines se développant avec les bourgeons floraux, a été suggérée en tant que principale responsable de l'abscission de bourgeons. Bien que le N de la feuille soit corrélé avec la rétention des bourgeons, l'application foliaire de N n'a pas réduit la chute de bourgeons. Les bourgeons floraux sur les branches sans fruits ont accumulé deux fois plus de ¹⁴C - photosynthate que ceux sur les branches portant des fruits. Un épuisement des hydrates de carbone dans des bourgeons floraux dans les arbres en année productive a été trouvé par quelques chercheurs pendant le développement des graines. Le mouvement du sucrose des feuilles aux bourgeons floraux a été également réduit, ayant pour résultat une diminution du développement des bourgeons floraux sur les arbres en année productive, qui a été suivie d'abscission. La possibilité que l'épuisement des hydrates de carbone dans plusieurs organes des arbres en année productive déclenche l'abscission de bourgeons pendant le développement des graines avec pour résultat l'alternance de production, est en passe d'être revue.

Mots-clés. Pistachier – Alternance de production fruitière – Abscission de bourgeon – Nutriments – Hydrates de carbone – Hormones.

I – Introduction

Alternation is a very widespread phenomenon occurring in both deciduous and evergreen trees. It appears in plant species with wide differences in dormancy, time of flower formation and flower habit, indicating that alternation is an inherent characteristic in polycarpic plants (Monselise and Goldschmidt, 1982). Alternate bearing or irregular bearing is the phenomenon by which trees bear an irregular crop year after year, usually heavy yields which are followed by light ones. In 'biennial bearing', however, the trees follow a biennial cycle of fruit production, thus an "on" year with large yields is followed by an "off" year with little or no yield. Amongst external

causes of alternation, climatic and edaphic stresses are the most important. The main effect of these stresses is the reduction of flowers or fruitlets one year followed by extensive shoot growth and fruit load in the following year. The main internal factor is the inhibition of flower initiation by the growing fruit, mainly due to the presence of hormones such as auxins and gibberellins in the developing seeds of the fruit (Hood, 1978). In most alternate bearing species, the presence of fruit is the key factor controlling flower initiation.

The purpose of this paper is to review the factors affecting floral bud abscission and alternate bearing in pistachio, with particular reference to the role of carbohydrate.

II – The unusual phenomenon of alternate bearing in pistachio

In contrast to other crop species, pistachio produces an abundant number of inflorescent buds every year which abscise mainly on fruiting trees or branches during the period of seed development. The pistachio is truly biennial as inflorescent bud abscission usually exceeds 95%. Many efforts have been made to explain this unusual phenomenon, but the mechanisms are still unknown; hence it remains a problem of significant commercial importance. It has long been known, however, that the presence of fruit and, in particular, seed growth is responsible for inflorescent bud abscission and for inducing a biennial bearing pattern (Crane and Nelson, 1971).

Flower initiation in pistachio begins in late April-early May, with flowers forming continuously until early July in both fruiting and non-fruiting trees. Then the process stops and recommences in early October with pistil initiation, stops again in winter and is completed a few days before bloom in late March (Takeda *et al.*, 1979). Bud abscission occurs in both fruiting and non-fruiting trees and is a two-phase process (Crane and Iwakiri, 1987). The first phase (30-38% bud-drop in 'Kerman' c.v.) occurs during the initial 5- to 6-week period of fruit growth in both "off" and "on" trees. This period coincides with the lignification of the endocarp and was attributed to a stimulus originating from the roots. The second and severe phase occurs only in fruiting trees during the 10- to 12-week period of fruit growth. This period coincides with rapid seed growth.

1. Factors affecting bud abscission in pistachio

Cultivar. Variation between cultivars in % bud abscission has been reported (Crane and Nelson, 1971); Esmailpour and Khezri (2006) studying four different cultivars found significant differences between them in bud abscission.

Rootstock. Tree to tree variations in the same orchard have been attributed to genetic differences between the seedling rootstocks used (Johnson and Weinbaum, 1987).

Fruit load. The more fruit present on shoots or branches, the more buds drop (Porlingis, 1974); fruit removal can result in inflorescent bud retention (Porlingis, 1974; Wolpert and Ferguson, 1990; Caruso *et al.*, 1992; Vemmos, 2005). The number of fruit per branch was found to be correlated to floral bud abscission (Wolpert and Ferguson 1990; Caruso *et al.* 1996). Fruit load on a branch can also affect the bud abscission on a neighbouring branch. It was also found that even 20 fruits per shoot can induce up to 100% bud abscission (Crane and Nelson, 1971; Porlingis, 1974).

Soil effect. Soil heterogeneity and its capacity for water and nutrients might affect tree growth and yield (Johnson and Weinbaum, 1987).

Leaf area. Inflorescent bud abscission increased with a decrease in leaf area per branch (Crane *et al.* 1973; Porlingis, 1974).

2. Bud abscission in pistachio and possible hormonal involvement

The abscission process is a very complex phenomenon and has been studied in several plant organs (e.g. leaves, fruits, flowers) in various species. In most cases of abscission studied, a sequence of biochemical events leads to wall break down in two or three layers of cells close to the point of detachment (Sexton and Roberts, 1982). The start of the abscission process is marked by increased respiration that stimulates higher rates of RNA and protein synthesis (Addicott, 1982; Sexton and Roberts, 1982). The abscission zone in floral buds of pistachio is similar to other organs in pistachio and other fruit trees (Lin *et al.*, 1984a). Division occurs in 2 to 3 cell layers in the cortex, pith, epidermis and parenchyma.

A hormonal factor produced in leaves or seeds moving to floral buds, acting on the bud base and triggering abscission was initially suggested (Crane *et al.* 1973; Porlingis, 1974). ABA levels in buds on fruiting and non-fruiting branches were found to be similar indicating that ABA is not a hormonal stimulus of bud abscission in pistachio (Takeda and Crane, 1980). Gibberellins (GAs) were found to be involved in abscission in some explants (Valdovinos, 1975). When GAs were applied to inflorescent buds of pistachio they induced abscission even in non-fruiting trees, thus indicating a possible role of GAs in bud abscission (Lin *et al.*, 1984b). Since no GA-like substances were detected in floral buds in "on" or "off" year trees, it was concluded that GA-like substances are not involved in bud abscission (Lin *et al.*, 1984c).

Vemmos *et al.* (1994) studied the role of ethylene in bud abscission and found that the production of ethylene by the buds of fruiting trees did not differ from that of non-fruiting ones. Despite this, the respiration rate in buds of fruiting trees was significantly higher than that in non-fruiting trees. This is in agreement with previous results showing that the start of abscission in leaves and fruit is marked by increased respiration rate (Addicott, 1982; Sexton and Roberts, 1982).

Various auxin applications have also been studied but none of these plant hormones have been directly implicated in bud abscission (Mouloulis, 1959; Crane and Nelson, 1972; Pontikis, 1990). It is also reported that parachlorophenoxyacetic acid (PCPA) and 2,4-dichlorophenoxyacetic acid (2,4-D) are possibly effective anti-abscission agents for pistachio inflorescent buds (Cawad and Ferguson, 1987a,b).

Latest results have shown that the concentrations of two cytokines, zeatin riboside and isopentylaniline each decreased by 40% in floral buds on shoots of "on" year trees while that of ABA increased by 25% between June 6 and July 26 in floral buds of the same trees (Lovatt and Ferguson, 1994). These findings conflict with previous results for ABA (Takeda and Crane, 1980), thus the role of ABA in bud abscission must be further investigated. Foliar application of 6-benzyladenine (25 mg l^{-1}) in combination with urea (two treatments) increased cumulative yield for four years in 'Kerman' pistachio by 23%, while a three-fold increase in cumulative yield was found for the two "off" year crops (Lovatt and Ferguson, 1994). Application of the same treatment on Aeginis cv. for two continuous years also increased yield, but to a lesser extent, and delayed bud abscission (Vemmos *et al.* unpublished data). However, the final percentage of bud drop was the same as in the untreated trees. In contrast, Talaie *et al.* (2006) found that 6-benzyladenine treatments (0, 25, 50, 100 mg l^{-1}) in combination with urea significantly reduced the final bud abscission in 'Ohadi' cv. These results, in combination with those of Lovatt and Ferguson (1994), indicate that the effect of this treatment is markedly dependent on the cultivar.

3. Nutrition and alternate bearing in pistachio

The competition between nuts and floral buds for nutrients and especially for nitrogen (N) was initially suggested to be a factor responsible for bud abscission (Anagnostopoulos, 1938). Nitrogen concentrations in floral buds during the period of fruit development and bud abscission were found to be similar or occasionally higher in buds of fruiting trees than in non-fruiting ones,

suggesting no relationship of N to flower abscission (Porlingis, 1974). N concentrations in leaves were found to positively correlate with the final bud retention (Wolpert and Ferguson, 1990). However, foliar N application did not alter bud abscission in fruiting trees. Pistachio trees that were "off" in the previous year reserved 144% and 22% more starch and N respectively than did trees that had been "on" (Weinbaum *et al.*, 1994).

The presence of fruit can affect nutrient uptake, utilization and distribution within various organs of fruit trees (Weinbaum *et al.*, 1994). In pistachio N and K uptake increased by 35 and 112% respectively during nut fill compared with "off" year trees indicating that sink demand regulates the uptake and distribution of these nutrients in pistachio (Rosecrance *et al.*, 1996). Caruso *et al.* (1996) found that the highest rate of nutrient accumulation in infructescences occurred during rapid embryo growth. The increased demand for nutrients by infructescences, particularly for N and K, is probably responsible for the lower concentrations of these nutrients in leaves of "on" year trees than "off" trees as found by Piccioni *et al.* (1997) and Vemmos (1999a). The presence of fruit significantly increased concentrations of Mg, Ca and Mn while that of K decreased in leaves and floral buds, however, N concentrations were higher in buds of bearing trees (Vemmos, 1999a), similar to the findings of Porlingis (1974). Although nutrient deficiency does not appear to be involved in bud abscission, the role of N and K in alternation needs further investigation.

4. The role of carbohydrates in bud abscission

The role of carbohydrates in inflorescent bud abscission in pistachio has been extensively investigated. Initially, Crane *et al.* (1976) and Crane and Shalan (1977) found that sugar and starch concentrations were similar in fruiting and non-fruiting branches, suggesting no relationship between carbohydrates and bud drop. The effect of developing kernel (seed) on translocation and distribution of photosynthates from leaf source to other parts of the tree was studied by Takeda *et al.* (1980) in defruited and fruiting trees. However, they found the presence of fruit did not affect the amount of ¹⁴C taken up by leaves. In contrast, fruit had a significant effect on the distribution of ¹⁴C-assimilates from leaves to other parts. Inflorescent buds on defruited trees grew more rapidly and accumulated twice as much ¹⁴C-photosynthate as those on fruiting ones, indicating that carbohydrate deficiency is possibly responsible for bud drop. This work, however, was limited to measuring the level of carbohydrates in the buds themselves. These very important results were in contrast to earlier findings (Crane *et al.*, 1976; Crane and Al Shalan, 1977). Based on the results of Takeda *et al.* (1980), Crane and Iwakiri (1987) suggested that the second phase of bud drop coinciding with the period of rapid seed growth was possibly due to carbohydrate deficiency in flower buds.

Increased Pn rates (up to 21-23% higher) were found in fruiting trees during the first stage of fruit growth and before the beginning of the second phase of bud abscission. From the time the seed growth begins, coinciding with the high rate of bud abscission, Pn rates were found to be similar in fruiting and non-fruiting trees in two continuous years measured (Fig. 1; Vemmos, 1994). These results indicated that the increased demand of carbohydrates during the seed development cannot be satisfied by an increase in leaf photosynthesis.

Nzima *et al.* (1997a) found that individual leaf area, leaf dry weight and specific leaf area (g cm⁻²) in fruiting branches were lower than those of non-fruiting trees but the total leaf area per branch was higher in fruiting branches. They also found that the distribution of total dry mass in fruiting branches from April to September was only 0.1% in inflorescent buds while that in non-fruiting branches was 1%. The total dry mass in fruiting branches in September reached 83.9 g while that in non-fruiting branches only 29.8 g. Studying the seasonal changes of soluble sugars, the concentrations of soluble sugars and starch found in all tree parts was much higher in the "on" trees up to 60 days after full bloom (AFB), but after this time, the concentration of starch declined in all parts of "on" trees while that of "off" trees continuously increased (Nzima *et al.*, 1997b). Similar results were obtained for soluble sugars in leaves and inflorescent buds but this did not apply for the wood of other parts (shoots and roots) where "on" and "off" trees had

similar concentrations. The results for soluble sugars in the wood were in agreement with the results of Crane *et al.*, (1976) and Crane and Al Shalan, (1977).

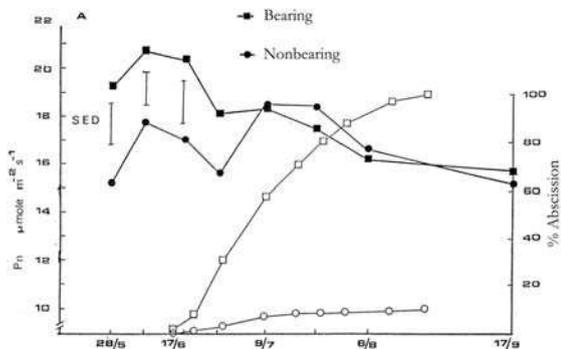


Fig. 1. Pn and bud abscission in bearing and non-bearing trees (Vemmos, 1994).

Anatomical investigations indicated that the event triggering the onset of the abscission process precedes the phase of rapid embryo development and that it might be ascribed to the embryo in the phase following the first zygotic division (Caruso *et al.*, 1995). Although the importance of carbohydrates in inflorescent bud abscission was shown (Takeda *et al.* 1980; Nzima *et al.* 1997b), the role of individual sugars in inflorescent bud growth and abscission was limited.

The changes in individual sugars and starch in floral buds on fruiting and defruited branches were studied (Vemmos, 1999b) and the most significant differences were found in sucrose and starch (Figs 2 and 3). Floral buds on defruited branches accumulated much more starch and sucrose than those of fruiting trees and grew faster from 55 days AFB, reaching 30% higher DW than the buds on fruiting branches. Since sucrose is the major translocated sugar in plants (Zimmermann, 1960; Ho and Baker, 1982), the rapid decrease in sucrose concentrations in buds of fruiting branches indicates a sucrose movement from buds to other parts of the tree. These results, in combination with the high carbohydrate demand of seeds in the same period, the decrease in Pn rates in leaves (Vemmos, 1994) and the decrease in the rate of bud growth, indicate that sucrose plays an important role in bud abscission.

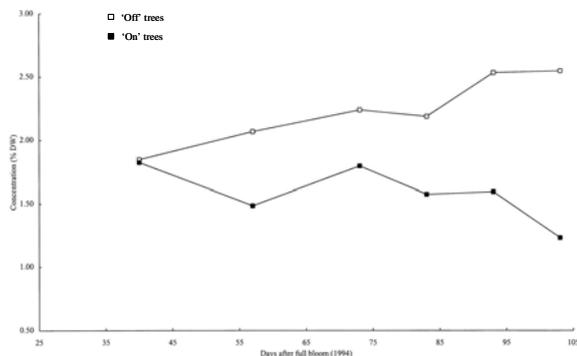


Fig. 2. The effect of fruiting on starch concentrations in "on" and "off" year pistachio trees (Vemmos, 1999b).

Baninasab and Rahemi (2006) confirming the above results, additionally showed that sucrose

and starch concentrations in roots of "on" trees were also much lower than those in roots of "off" trees during bud abscission, indicating a possible starch mobilization and sucrose movement from roots to other parts of the tree. They also found a negative correlation between carbohydrate content and bud abscission.

Finally, Spann *et al.* (2008) analyzed annual carbohydrate storage and mobilization of bearing and non-bearing 'Kerman' pistachio trees growing on three different rootstocks. They found that in "on" trees', carbohydrates increased temporarily in early summer but they were mobilized in mid season during kernel fill and then increased again after the nut harvest. They concluded that mobilization of carbohydrates from current season and 1- and 2-year-old stem wood of "on" trees during the primary period of kernel fill corresponded with the period of inflorescent bud abscission.

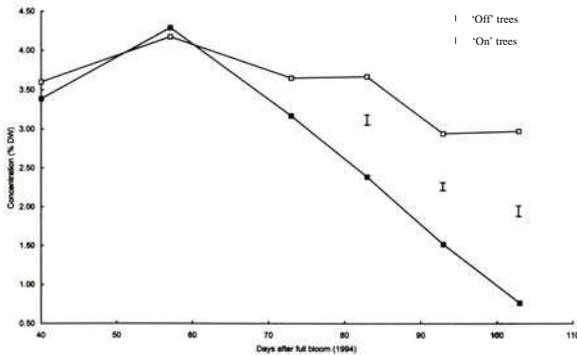


Fig. 3. The effect of fruiting on sucrose concentrations in "on" and "off" year pistachio trees. Vertical bars indicate SED. (Vemmos, 1999b).

A. Treatments affecting carbohydrate levels within the tree and bud abscission

Girdling of shoots or branches causes a series of physiological changes above the ring, such as reduced growth, accumulation of carbohydrates and/or other organic substances, while affecting the hormonal balance of the shoot (Stoltz and Hess, 1966a,b; Goldschmidt and Huber, 1992; Hartman *et al.*, 2002). In pistachio, girdling between inflorescences and current shoots before bud abscission resulted in a significant reduction of bud drop (Crane and Nelson, 1972).

Girdling individual shoots at the base of the current shoot (girdle I, Fig 4), thus separating inflorescent buds on the terminal current shoot from the developing fruits, reduced inflorescent bud abscission by 62-66% in comparison to untreated controls (Vemmos, 2005). In contrast, both girdling at the base of one-year old shoots (girdle II) and fruit removal treatments reduced bud abscission only by 20 and 16% respectively in 1994).

Girdle I increased dry weight of floral buds and minimized the fruit competition for carbohydrates which caused carbohydrate accumulation in all organs above the ring (including buds) and this was correlated with bud retention. Girdle I also reduced Pn rates by 70% at 10 days after the treatment while girdling at the base of 1-year-old shoot (girdle II) did not affect Pn (Vemmos *et al.* unpublished data). Thus, the presence of fruit is a strong assimilate sink in pistachio and therefore may regulate the source–sink of assimilates within the shoot and control leaf Pn rates.

Treatments that reduced leaf area on non-fruiting branches increased % bud abscission. Complete defoliation had the most detrimental effect on bud abscission (similar to that occurring on bearing branches) but all the other defoliation treatments had a similar and smaller effect

(~30% bud abscission; Crane *et al.*, 1973). However, when the number of fruits increased from 0 to 10 or 20 fruit per branch, % bud abscission increased and was dependent on the level of leaf removal. These results were partly attributed to the limitation of carbohydrates supplied by the leaves.

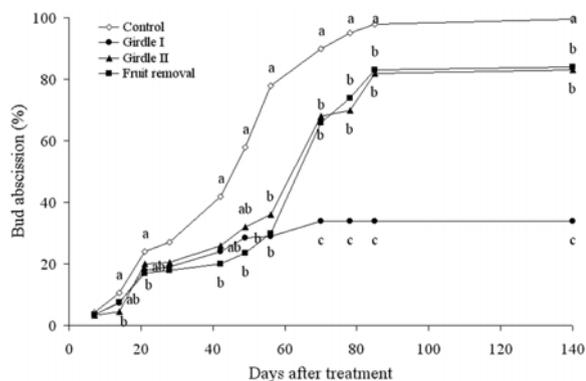


Fig. 4. The effect of girdling and defruiting on bud abscission of pistachio trees Vemmos (2005). Different letters indicate significant differences ($p < 0.05$).

Early fall defoliation treatments of "off" and "on" year pistachio trees reduced carbohydrate reserves and suppressed initial leaf area in the following spring of "off" year but not of "on" year trees. Consequently, the carbohydrate level in organs of defoliated trees was lower than the control (Nzima *et al.*, 1999). Additionally, early June shading of "on" and "off" trees for 14 days reduced the total non-structural carbohydrates in individual leaves, inflorescent buds, current year and 1-year-old shoots and this carbohydrate reduction was correlated with bud abscission.

III – How to reduce alternation in pistachio

In order to reduce bud abscission and increase yield in pistachio the following aspects must be taken into consideration.

Cultivar and rootstock selection and improvement. These must aim to give vigorous trees with a high ratio of leaf area/fruits, high photosynthetic capacity and an increased ability to store large amounts of carbohydrate and nutrients in the aerial parts of the tree. The selected cultivars should also have a reduced alternate behaviour with high productivity and good kernel quality. The ability of the selected rootstock to be propagated by asexual methods (cuttings, micropropagation) is very important for its commercial use.

Orchard management. Appropriate pruning to regulate fruit load and increase the ratio of leaf area/fruits is necessary to improve yield in pistachio orchards. Appropriate nutrient application, particularly nitrogen and potassium, and supply to leaves during the period of seed growth, in combination with sufficient irrigation might reduce alternation. Foliar application of nitrogen in combination with cytokines in order to increase sink strength in floral buds and delay leaf senescence might reduce bud abscission and alternation in pistachio. Finally, foliar application of other hormones (auxins) to reduce floral bud abscission must be further investigated.

IV – Conclusions

(i) The phenomenon of alternate bearing in pistachio is unique. Floral bud abscission, caused mainly by the presence of fruit, is responsible for alternate bearing.

(ii) The extent of the effect of bud abscission and alternation is influenced by cultivar while rootstock can also affect alternation in pistachio.

(iii) Fruit production in an "off" year is dependent on the size of the fruit load in the "on" year.

(iv) The second and most severe phase of bud abscission coincides with the period of embryo and seed development. During this period, a great demand for carbohydrates and nitrogen for protein synthesis exists.

(v) Seeds operate as strong sinks (possibly hormonally mediated) for carbohydrate and nutrients, while floral buds compete poorly with strong sinks (fruits) for assimilates, nitrogen and possibly other nutrients.

(vi) A depletion of carbohydrate and some nutrients occur in several parts of the tree during nut fill that coincides with the second, severe phase of bud abscission.

(vii) Sugar (possibly sucrose) movement from leaves to floral buds is reduced on fruiting trees/branches leading to decreases or cessation in bud growth, resulting in bud abscission.

(viii) The important role of carbohydrates has been well demonstrated while the role of hormones in bud abscission is still unclear and needs further investigation.

(ix) Based on this review, in particular the results for carbohydrates, a series of events that possibly trigger bud abscission, similar to those suggested by Schneider (1977) for young fruit in apple and peach, is proposed (Fig. 5).

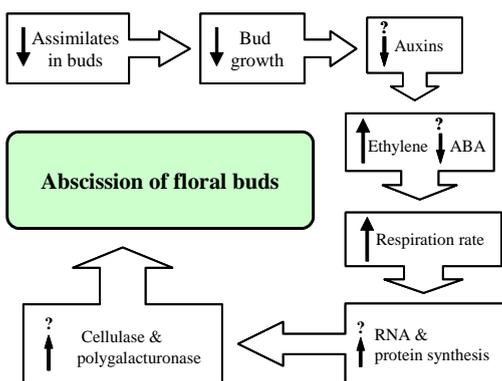


Fig. 5. The proposed process triggering bud abscission in pistachio.

According to this the following questions remain:

(i) What are the physiological and biochemical processes involved in carbohydrate deficiency-induced bud abscission?

(ii) Which other substances (including hormones) are also involved?

(iii) What is the exact role of auxins, ethylene and ABA?

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