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Possible Role of Non-Structural Carbohydrates in Alternate Bearing of Pistachio

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Summary

The alteration of heavy and light yield in pistachio (*Pistacia vera L.*) has been reported to result from the abscission of flower buds on heavily yielding trees during the summer, but the regulatory mechanisms involved in this bud abscission remain unclear. The present study was conducted to examine the role of nonstructural carbohydrates in flower bud abscission. Carbohydrates (glucose, fructose, sucrose and starch) content was measured in flower buds, leaves, fruits, current shoots, one year old shoots and roots of eight 'OFF' and eight 'ON' 30 year old pistachio cv. 'Owhadi' trees at monthly intervals between flowering and harvest. The flower bud abscission percentage was recorded every 15 day during seed growth. The amounts of soluble sugars and starch were relatively similar in many organs both in 'OFF' and 'ON' trees until 70 days after bloom. Thereafter, the amount of soluble sugars and starch in 'ON' trees declined in many organs during nut development. During the same period, various organs of 'OFF' trees began to accumulate greater concentration of soluble sugars and starch and surpassed the amount measured in those of 'ON' trees. There was a high and significant negative correlation between bud, leaf and root sucrose and fruit glucose and flower bud abscission. This indicates that soluble sugars in the many part of tree could be related to the alternate bearing in pistachio.

Key words. *Pistacia vera* L. – alternate bearing – flower bud abscission – nonstructural carbohydrates.

Introduction

Alternate bearing- the alternation between a high and low crop year- is very common among most fruit tree species including apple (Monselise and Goldschmidt 1982). Pistachio (*Pistacia vera* L.) is a strongly alternate bearing tree crop species, and yields vary 3 to 5 folds between heavy cropping ('ON') and subsequent light cropping ('OFF') years (Johnson and Weinbaum 1987). The mechanism involved in pistachio trees, however, seems to be different from that of other fruit tree species (Golan-Goldhirsh et al. 1998). Alternate bearing in many tree species such as e.g. apple is usually the result of greatly reduced flower bud formation during the year of a heavy crop. In contrast, in pistachio it is brought about by an unusual mechanism of flower bud abscission during the summer in which a heavy crop of nuts is being produced (Roussos et al. 2004). Two hypotheses have been proposed to explain alternate bearing of fruit trees in general, as well as flower bud abscission in pistachio: a) endogenous plant growth regulators or inhibitors of bud abscission produced either in the seed or leaves are respectively drawn towards or away from the buds leading to bud abscission or failure in bud initiation (Monselise and Goldschmidt 1982; Pontikis 1990) and b) carbon sinks compete for metabolites, especially carbohydrates and nitrogen, resulting in failure in initiation of reproductive buds or in the case of pistachio, in abscission of flower buds (Monselise and Goldschmidt 1982; Crane 1984; Garcia-Luis et al. 1988; Vemmos 1999).

The purpose of this study was to find out the quantitative relationship between the effects of crop load on seasonal patterns of nonstructural carbohydrates concentration in perennial and annual tissues of mature bearing and non bearing pistachio trees and also to provide information on the relationship between the abscission of flower buds and carbohydrate content among individual organs of pistachio trees.

Materials and Methods

Experimental trees

In summer 2003, sixteen 30 year old pistachio cv. 'Owhadi' trees which had been grafted on pistachio cv. Badami Riz' rootstock having for uniform size, crop load and canopy size were selected at the experiment station of the Iranian Pistachio Research Institute in Kerman region. Eight of the 16 trees were carrying a heavy crop of fruit in 2003 ('ON' trees) and a light crop in 2004 ('OFF' trees). The other 8 trees were 'OFF' in 2003 and 'ON' in 2004. Each tree had 3 primary scaffold branches. Standard commercial practices for weed control, fertilizer applica-

tion and irrigation scheduling were performed during the experiment. Full bloom occurred on 6th of April 2004.

Plant Sampling

Samples for carbohydrate analysis were taken from 'OFF' and 'ON' trees in 2004 between 1000 and 1200 h on each date to minimize diurnal effects. Samples were flower buds, leaves, fruits, current season and one-year-old shoots from four branches and also root samples (<10 mm in diameter). Root samples were collected from three, 30 cm holes dug at random 1 m apart from the trunk of each trees. The samples were collected on 16 April [10 days after full bloom (10 DAFB)], 16 May (40 DAFB), 15 June (70 DAFB), 15 July (100 DAFB), 14 August (130 DAFB) and 13 September (160 DAFB= harvest time). However, flower buds were collected from 40 DAFB until harvest time. These dates were selected to coincide with vegetative growth and increase in pericarp mass (April to May), lignification of the endocarp (May to June), seed growth and development (late June to August).

All samples were washed immediately in cold water and packed in ice for transfer to the laboratory to be kept at −20 °C for 24 h. Samples were then freeze-dried at −50 °C for 48 h in a freeze-dryer (FD1- Eyela, Tokyo, Japan) , then were ground using a Willey mill and passed through a 40-mesh screen and stored at −20 °C until analysed for carbohydrates.

Soluble sugars analyses

The method of VEMMOS (1995) was modified in the laboratory and used for sugar analysis as described below. Ground dried tissue (0.1 g) was placed in a centrifuge tube, 5 ml of 40–60 °C petroleum ether was added and centrifuged for 5 min at 3000 rpm. The petroleum ether extract, containing lipids, chlorophyll and other contaminants, was carefully pipetted off and discarded. Eighty percent (v/v) ethanol/ water (4 ml) was added to the tube and vortexed. The tube was placed in water- bath at 65 °C for 20 min. After centrifugation at 3000 rpm (5 min) the supernatant was pipetted to another centrifuge tube. The remaining plant material was then re-extracted with 4 ml of 80 % ethanol, centrifuged and the supernatant was added to the first one, before drying under a stream of nitrogen gas. Four ml distilled water was added to the dried residue in tube and the sugars were dissolved by shaking. Activated charcoal (10 mg) was added to the solution, mixed well and the mixture centrifuged at 3000 rpm for 5 min. After centrifugation, the supernatant was removed and filtered through a 0.45 μm membrane filter (Schleicher and Schuell, Dassel, Germany) prior to injection (10 μl) onto a 300×7.9 mm HPLC column (SCR-101 N, Shimadzu, Kyoto, Japan) at 60 °C. The mobile phase (deionized water), was supplied by an isocractic pumping system (LC- 6A, Shimadzu, Kyoto, Japan) at a flow rate of 0.7 ml min^{-1}. After separation, the compounds from the mixture were passed through a refractive index detector (RID-6A, Shimadzu, Kyoto, Japan) linked to a chart recorder (CRUA, Shimadzu, Kyoto, Japan). Each sample was assayed twice and sugars concentrations were expressed as mg g^{-1} dry weight (d.w.)

Mixed standards solutions containing glucose, fructose and sucrose, at concentrations of 100, 200, 500, 1000, and 2000 mg l^{-1} were injected onto the column and their peaks were used to construct calibration curves for each sugar. The concentration of individual sugars in each sample was then calculated using peaks and the calibration curves.

Starch analyses

The solid residue left in the centrifuge tube after the removal of soluble material was washed and recentrifuged four more time using 80 % ethanol/water. Total starch in samples was determined using a Total Starch Assay Kit (Cat. No. K-TSTA, Megazyme, County Wicklow, Ireland). The method consisted of hydrolysing starch to glucose enzymatically. Glucose was determined colorimetrically using glucose oxidase-peroxidase reagent.

Bud abscission records

On each of the tree, four randomly selected fruiting shoots (in 'ON' trees) and non-fruiting shoots (in 'OFF' trees) were selected. Bud abscission (calculated as percentage of flower buds abscised from the shoot) was recorded in 15-day intervals, beginning in 70 DAFB till the end of experiment. On each observation date, buds were touched lightly with fingertip to distinguish those that had formed abscission layer but remained lodged between the leaf petiole and the shoot.

Statistical analysis

The experiment was arranged as a randomised complete block with four replications and two trees per replication. Seasonal changes in carbohydrate composition were subjected to an analysis of variance using the date of sampling and fruiting state of the trees ('OFF' and 'ON') as variables. The residual sum of squares was used to calculate the standard error of the individual determination. Pearson correlation coefficient was calculated in order to determine the correlation between carbohydrate concentration and bud abscission. Statistical analysis was performed using MSTATC (Michigan State Univ., East Lansing).

Results

The pattern of flower bud abscission

The pattern of flower bud abscission was markedly affected by the fruiting state of the trees. The results in Fig. 1 show that more than 40 % of buds on 'ON' trees fell between 100 DAFB and 130 DAFB, reaching 92.3 % at 160 DAFB. On the other hand 'OFF' trees exhibited only 19.4 % bud abscission at 160 DAFB (Fig. 1).

Nonstructural carbohydrate levels in flower buds

The results of carbohydrate measurements in the growing flower buds show that initial concentration of various soluble sugars and starch were relatively similar in both 'OFF' and 'ON' trees (Table 1). With flower bud development, initially the sucrose concentration, and later starch concentration became much higher in buds of 'OFF' tree than in 'ON' ones. However, by the last sampling date,

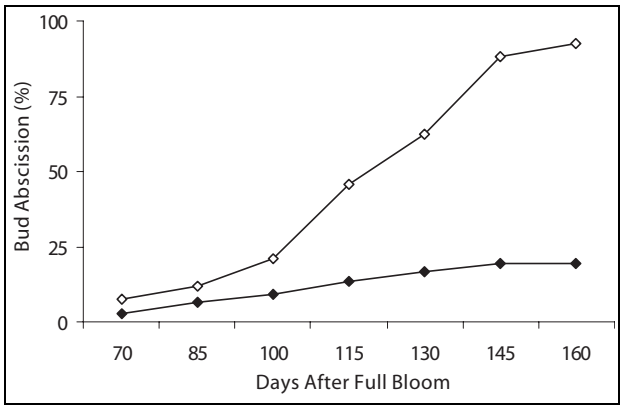


Fig. 1. Time course of flower bud abscission on 'OFF' (closed symbols) and 'ON' (opened symbols) pistachio trees. 'ON' = heavy cropping; 'OFF' = subsequent light cropping.

flower buds of 'OFF' trees had twice as much sucrose (45.18±0.52 vs. 20.71±0.71 mg g^{-1}) and 427.9 % more starch (18.4±0.8 vs. 4.3±0.3 mg g^{-1}) than buds of 'ON' trees. The glucose and fructose contents were not affected by the fruiting state of the trees, although in the 70 and 160 DAFB, buds on 'OFF' trees had significantly higher amount of glucose and fructose respectively, than those from 'ON' trees (Table 1).

Nonstructural carbohydrate levels in leaves

The concentrations of glucose and sucrose in leaves of 'ON' and 'OFF' tree increased at 40 DAFB. Thereafter, 'OFF' leaves contained more glucose and sucrose than 'ON' leaves (Table 1). The amount of fructose in leaves of 'ON' and 'OFF' trees were relatively similar until 70 DAFB, thereafter, its concentrations in leaves of 'ON' trees declined and that of 'OFF' trees continued to increase. The amount of starch increased from 10 to 130 DAFB in both 'ON' and 'OFF' trees without any significant difference between 'ON' and 'OFF' trees. However in last sampling date, starch content in leaves was 37.63 % (25.6 vs. 18.6 mg g^{-1}) greater in 'OFF' vs. 'ON' trees (Table 1).

Nonstructural carbohydrate levels in fruits

The amount of glucose decreased from 70 DAFB onwards in both 'OFF' and 'ON' trees, without any significant difference between fruiting and non-fruiting ones (Table 1). Fructose content of fruits remained relatively stable from the beginning of the season to 130 DAFB and sharply decreased at the last sampling time. The result show that fruits from 'OFF' trees generally had significantly higher fructose than 'ON' trees in most samplings. Sucrose content of the fruits of the both 'OFF' and 'ON' trees increased from the beginning of the season, reaching a maximum in 130 DAFB. Subsequently, sucrose concentration in fruits markedly decreased at the end of sampling time. Little difference was observed between the 'OFF' and 'ON' trees, although in 'OFF' trees sucrose content in fruits was higher than in the 'ON' trees. Starch fluctuation in fruits was more than other carbohydrates. At the last sampling date, starch concentration of fruits of 'ON' trees was 11.11 % higher than those of 'OFF' trees (Table 1).

Nonstructural carbohydrate levels in current shoots

In most samplings, current shoots from 'OFF' trees had significantly higher glucose content as compared with 'ON' trees (Table 1). Both fructose and sucrose content in current shoots, after their significant increase during the second and third sampling date decreased at 130 DAFB and thereafter increased again in both 'OFF' and 'ON' trees. However, there was no consistent significant difference in fructose and sucrose content of current shoots between 'OFF' and 'ON' trees in most sampling periods(Table 1). Starch content in the current shoots was at minimum early in the season and increased in both 'OFF' and 'ON' trees with time. However, the rate of the increase was higher in 'OFF' trees.

Nonstructural carbohydrate levels in one-year-old shoots

Glucose and fructose concentrations within one year old shoots of 'OFF' and 'ON' trees were relatively similar during the growing season (Table 1). Concentration of sucrose in the one year old shoots showed the same pattern for fructose. One year old shoots from 'ON' trees exhibited significantly higher sucrose than that of 'OFF' trees for all sampling times. Seasonal changes in starch concentration in one- year-old shoots of 'OFF' and 'ON' trees were relatively similar until 70 DAFB thereafter, the concentration in one year old shoots of 'OFF' trees continued to increase and that of 'ON' trees its remained constant (Table 1).

Nonstructural carbohydrate levels in roots

Roots of 'ON' trees had about twice the amount of glucose and fructose (8.14±0.58 and 4.97±0.22 mg g^{-1}, respectively) as those of 'OFF' trees (4.74±0.35 and 2.24±0.13 mg g^{-1}, respectively) at 10 DAFB (Table 1). Thereafter, half way through the experiment, roots from 'OFF' trees had higher glucose and fructose than those from 'ON' trees. However, at last sampling time, the amount of glucose and fructose in roots of both 'OFF' and 'ON' trees were similar. Changes in sucrose and starch content are presented in Table 1. Roots from 'OFF' trees generally had significantly higher sucrose and starch than that of 'ON' trees in most samples.

Relationship between carbohydrate concentration and bud abscission

As can be seen from Table 2, most of the variables used had a significant negative relation with the percentage of bud abscission. In most cases this negative correlation proved to be quite strong, like sucrose in buds, leaves and roots and starch in roots.

Discussion

Results showed that 'OFF' trees had 19.41 % bud abscission during the development of the seed on the nearby 'ON' trees. On the other hand, the latter exhibited a higher rate of flower bud abscission. These results are in agreement with those reported by Porlingis (1974) and Takeda et al. (1980) who found that bud abscission occurs in both fruiting and non-fruiting trees. However, bud ab-

Table 1. Seasonal changes in the nonstructural carbohydrates content (mg g^{-1}) in flower buds, leaves, fruits, currents shoots, one-year-old shoots, and roots of 'OFF' and 'ON' trees of pistachio trees. Data are means ± s. e. (n=4).

DAFB	'OFF' trees				'ON' trees			
	Glucose	Fructose	Sucrose	Starch	Glucose	Fructose	Sucrose	Starch
Flower buds								
40	4.24±0.20	18.89±0.71	35.14±1.05	1.21±0.03	4.56±0.14	18.14±0.44	37.01±0.62	1.09±0.16
70	4.89±0.16	20.14±0.67	40.53±0.74	0.59±0.09	4.28±0.17	18.56±0.66	35.10±0.65	0.97±0.10
100	4.37±0.08	19.33±0.79	44.41±0.94	0.83±0.08	4.40±0.13	20.17±0.85	30.79±0.74	0.53±0.08
130	4.76±0.08	21.67±0.22	42.91±1.20	1.03±004	4.85±0.14	21.45±0.66	23.31±0.80	0.60±0.10
160	4.96±0.06	23.79±0.74	45.18±0.52	1.84±0.08	4.93±0.02	21.88±0.70	20.17±0.71	0.43±0.03
Leaves								
10	5.46±0.48	4.22±0.25	8.78±0.62	0.19±0.01	4.58±0.52	4.96±0.36	9.46±0.69	0.24±0.04
40	8.24±0.68	4.62±0.49	16.28±0.75	1.83±0.01	8.82±0.71	4.92±0.49	16.11±0.79	1.80±0.10
70	8.84±0.35	5.58±0.69	18.90±0.40	2.47±0.21	6.34±0.74	5.28±0.56	14.42±0.71	2.29±0.16
100	9.82±0.58	7.62±0.15	19.68±0.74	2.40±0.17	6.64±0.48	4.16±0.20	11.26±0.16	2.31±0.29
130	10.22±0.16	7.88±0.12	20.26±0.74	2.37±0.19	5.22±0.35	2.44±0.19	7.62±0.43	2.52±0.02
160	10.62±0.33	8.98±0.36	23.32±0.46	2.56±0.19	6.26±0.11	3.04±0.32	9.84±0.81	1.86±0.30
Fruits								
10	4.22±0.17	13.41±0.39	18.92±0.50	0.39±0.02	4.08±0.03	11.97±0.56	19.64±0.59	0.43±0.01
40	7.17±0.47	17.82±0.64	20.71±0.43	0.52±0.07	8.14±0.37	12.86±0.91	22.81±0.99	0.60±0.07
70	8.76±0.37	15.64±0.32	49.56±2.78	0.56±0.03	9.23±0.33	14.46±0.35	46.15±2.02	0.44±0.02
100	7.25±0.29	13.99±0.48	107.94±3.50	0.95±0.04	6.61±0.34	12.81±0.13	100.61±2.80	0.80±0.04
130	3.64±0.21	10.17±0.60	129.94±3.08	0.60±0.05	3.46±0.18	11.64±0.46	121.94±2.89	0.42±0.02
160	2.96±0.27	4.41±0.11	35.86±2.91	0.54±0.05	2.58±0.20	3.74±0.23	30.42±2.40	0.66±0.03
Current shoots								
10	7.13±0.42	4.16±0.26	10.23±0.67	0.62±0.05	6.79±0.47	4.65±0.38	14.53±0.43	0.16±0.01
40	15.18±0.68	14.52±0.74	25.78±0.70	2.22±0.15	8.95±0.42	13.09±0.46	27.03±0.57	1.97±0.13
70	10.49±0.82	11.14±0.43	30.41±1.07	5.43±0.44	7.11±0.16	10.49±0.45	29.58±0.59	5.26±0.61
100	10.52±0.37	10.62±0.30	22.89±0.52	8.54±0.24	8.45±0.76	10.52±0.41	24.66±0.64	5.00±0.10
130	6.26±0.17	6.26±0.16	17.09±0.31	10.70±0.35	6.43±0.32	6.43±0.30	18.11±0.65	5.95±0.29
160	12.41±0.34	12.18±0.48	25.64±0.45	10.43±0.66	11.32±0.30	11.99±0.67	22.36±0.42	9.35±0.62
One-year-old shoots								
10	9.31±0.31	7.42±0.27	14.81±0.39	5.49±0.62	9.68±0.52	7.03±0.13	17.14±0.63	3.58±0.29
40	16.94±0.32	13.21±0.32	20.44±0.33	4.28±0.05	17.52±0.12	14.11±0.62	23.71±0.36	3.00±0.07
70	13.44±0.25	14.61±0.54	26.39±0.17	6.42±0.04	12.64±0.27	14.52±0.13	30.82±0.66	5.61±0.83
100	8.83±0.28	6.64±0.29	11.17±0.12	8.09±0.36	8.31±0.26	5.21±0.45	14.29±0.43	5.61±0.34
130	6.36±0.43	4.13±0.27	5.61±0.16	8.56±0.11	6.52±0.30	4.52±0.37	8.93±0.46	5.10±0.32
160	12.53±0.30	7.49±0.19	13.78±0.31	8.60±0.21	11.72±0.33	6.80±0.26	16.78±0.51	5.50±0.53
Roots								
10	4.74±0.35	2.24±0.13	14.16±0.97	7.81±0.92	8.14±0.58	4.97±0.22	18.51±0.92	10.47±0.32
40	8.44±0.69	3.47±0.39	35.26±1.43	10.54±0.13	7.29±0.44	3.32±0.32	18.90±1.05	4.08±0.40
70	9.01±0.57	4.35±0.27	37.14±1.08	9.80±0.35	5.28±0.31	2.07±0.10	26.42±0.92	8.32±0.16
100	9.63±0.71	5.53±0.20	42.32±1.47	11.02±0.76	7.01±0.31	3.55±0.30	36.24±0.71	4.49±0.16
130	4.37±0.33	2.36±0.10	31.16±0.85	7.05±0.42	5.35±0.62	2.60±0.24	21.81±0.95	2.58±0.14
160	5.90±0.38	1.87±0.09	32.82±0.93	7.55±0.10	5.60±0.22	1.92±0.85	24.23±0.81	4.35±0.25

DAFB = Days After Full Bloom.
'ON' = heavy cropping; 'OFF' = subsequent light cropping.

scission in fruiting trees is usually much less and generally does not exceed 20–30 % of total buds.

In this study, carbohydrate contents varied among the tree parts as a result of alternate bearing. Results showed

Table 2. Correlation coefficients between the various variables (sugars concentration in different organs) and the percentage of flower bud abscission in pistachio trees.

Variables	Buds	Leaves	Fruits	Current shoots	One-year-old shoots	Roots
Glucose	ns	−0.53**	−0.66**	ns	ns	−0.36*
Fructose	ns	−0.65**	ns	ns	−0.41*	−0.46**
Sucrose	−0.82**	−0.68**	ns	−0.45*	ns	−0.68**
Starch	−0.38*	−0.42*	ns	ns	−0.44*	−0.72**

* P<0.05, ** P<0.01, ns = not significant

that sucrose was the predominant soluble sugar in different pistachio tree parts tested.

Although glucose and fructose contents were relatively similar in buds of 'OFF' and 'ON' trees, sucrose and starch concentrations dropped from 70 DAFB in 'ON' trees, coinciding with the start of high rate of flower bud abscission. A decrease in starch concentration during the same period in the buds of 'ON' trees can be attributed to mobilization of reserve carbohydrates for flower bud growth i.e. starch conversion to other sugars as indicated by the increase in glucose and fructose content during the same period (Table 1). The decrease in sucrose concentration in flower buds of 'ON' trees may result from a combination of poor competition for sucrose (Takeda et al. 1980) or due to inefficient use of accumulated photoassimilates (Nzima et al. 1997b). It is well known that sucrose is the major translocated sugar in the most of plants (Ho and Baker 1982). Since fruits are known to be strong sink of carbohydrate, it is likely that sucrose moved from flower buds to the fruits. Takeda et al. (1980) also found that buds on individual fruiting shoot accumulated 50 % ^{14}C-labeled photosynthates as compared to those on individual defruited shoots.

In the present study, leaves of 'OFF' and 'ON' trees accumulated soluble sugars (mainly glucose and sucrose) until about 40 DAFB, thereafter, soluble sugars content in leaves of 'ON' trees declined and that of 'OFF' trees continued to increase. This suggests that leaves on 'ON' trees start the growing season as sink although this seem unlikely in view of the possible competition from developing fruitlets and current year shoots. Nzima et al. (1997b) found that 60 % of pistachio nuts had abscised by 30 DAFB, which coincided with accumulation of soluble sugars in leaves of 'ON' trees. Alternatively, developing leaves of 'ON' trees may have been stronger sinks compared to developing fruitlets resulting in the observed greater leaf area which has been reported earlier (Nzima et al. 1997a). Schaffer et al. (1985) also showed that the young developing leaves serve as competitive sinks for available metabolites. In the present experiment, the amount of soluble carbohydrate in the leaves of 'ON' trees rapidly decreased from 40 and 70 DAFB to 130 DAFB. These results combined with those of Nzima et al. (1997*b*) indicates that young leaves of 'ON' trees undergo a sink to source transition as the season progresses. Similar shifts in sink-source relation have been reported for many other plant species (Schaffer et al. 1985; Hansen 1989). However, leaves of 'OFF' trees had greater soluble sugars and starch than of 'ON' trees at the end of experiment. Our results were in agreement with those reported by Nii (1997) who found that leaves of fruiting trees had lower content of carbohydrate than defruited trees.

The growth and development of pistachio fruits start well before leaf photosynthetic competence and continues almost till harvest (Nzima et al. 1997b). Fruit contained greater amount of carbohydrates than any other organs. Nzima et al. (1997b) suggest that developing fruits derive their carbon requirements from current photoassimilates and stored reserves. Sucrose presented in much greater quantities than the other carbohydrates components throughout growth and development of the fruit. In the present study, the amount of sucrose increased markedly in fruits which coincided with a decline in concentration of both some soluble sugars in buds, leaves, current and one year old shoots and also starch in buds and roots. These could mean that carbohydrate concentration decreases significantly, because of translocation to fruits. In contrast to the heavily producing 'ON' trees, the 'OFF' trees in the absence of fruit sinks accumulated carbohydrates in individual organs. Thus the immense demand for carbohydrates by developing fruits in 'ON' trees established them as the major sink, whereas in the other organs there is a shift from sink to source as the season progresses (Nzima et al. 1997b). However in our study, sucrose initially increased sharply, reaching a peak at 130 DAFB and thereafter declined rapidly. This result and the one reported by Crane (1986) indicate that a sharp decrease in sucrose during the last sampling period coincides with the beginning of fat accumulation in seeds. Crane et al. (1976) found that a rapid increase in crude fat commenced as total sugar began declining during seed growth.

Current shoots starch content increased progressively during the experiment. However, at each sampling date, starch content in the current shoots of 'OFF' trees was higher than that of 'ON' trees. Nzima et al. (1997b) found that next to nuts, current woods were probably the second strongest sinks in an individual branch. Crane et al. (1976) found no differences in soluble sugars and starch in current wood of 'OFF' and 'ON' trees. Several other independent studies found greater total amounts of carbohydrates in 'OFF' than 'ON' trees (Monselise and Goldschmidt 1982; Kappel 1991; Nzima et al. 1997b).

The concentration of starch among roots ranged from a seasonal low of 2.58 to 10.47 % in 'ON' trees and from 7.05 to 11.02 % in 'OFF' trees. These values were similar with starch content of one-year-old shoots and were lower than what is found in current shoots. Most published

report indicates greater concentration of starch in roots than in shoot organs (KRAMER and KOZLOWSKI 1979; LOESHER et al. 1990). This discrepancy may be due to the different sizes of roots that were analysed in various studies (NZIMA et al. 1997b). The high concentration of carbohydrate in roots of 'ON' trees early in the season is probably due to carbohydrate accumulation during the previous 'OFF' year, while the decrease during seed development is possibility due to high carbohydrate requirement by seeds for fat synthesis.

In the present study carbohydrate exhibited a negative relation with flower bud abscission. Branch girdling between developing nuts and the flower buds reduced bud abscission at about the same level as the one on branches from which all young nuts were removed. This indicated that competition between nuts and buds for carbohydrates might be responsible for abscission of the buds (CRANE and NELSON 1972). TAKEDA et al. (1980) have shown that, developing nuts may be the strongest sinks, as they have the highest amount of recently fixed ^{14}C-photosynthates as compared to other organs on the branch, which were tested.

Conclusion

In conclusion, in most cases, carbohydrate concentrations were significantly lower in organs of 'ON' trees (presenting major bud abscission) than of 'OFF' trees. This along with the negative correlation between carbohydrates and bud abscission could mean that when carbohydrates content decrease below a specific level, it could trigger the abscission mechanism. Overall, the most likely candidate to cause alternate bearing in pistachio is the sucrose in the buds and leaves, followed by starch in roots by correlation coefficient.

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