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# Seasonal Changes in Total Nonstructural Carbohydrates within Branches and Roots of Naturally "Off" and "On" 'Kerman' Pistachio Trees

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**ABSTRACT. The objective of this investigation was to determine the dynamics of carbohydrate use as revealed by soluble sugar and starch concentration in leaves, inflorescence buds, rachises, nuts, current and 1-year-old wood, and primary and tertiary scaffold branches and roots (≤10 mm in diameter) of alternate-bearing 'Kerman' pistachio (*Pistachia vera* L.) trees that were in their natural bearing cycles. Two hypotheses were tested. First, carbohydrate concentration is greater early in the growing season in organs examined from heavily cropping ("on") than light cropping ("off") trees. This hypothesis was affirmed as judged by soluble sugar and starch concentration in leaves, inflorescence buds, rachises, nuts, current and 1-year-old wood, and primary and tertiary branches and roots of "on" compared to "off" trees. Second, carbohydrate concentration remains high in "on" tree organs as the first wave of inflorescence bud and nut abscission occurs early in the growing season. This hypothesis was also affirmed. In fact, soluble sugars and starch remained high in "on" trees through full bloom FB + 60 days (FB + 60) as inflorescence bud and nut abscission occurred. In the persisting "on" tree inflorescence buds, sharp decreases in soluble sugars and starch were evident by the final sample date when "off" tree inflorescence buds contained a 13 times greater concentration of soluble sugars and starch than "on" tree buds. At that time, "off" tree inflorescence buds contained 50% more dry mass than "on" tree inflorescence buds. After FB + 60, "on" tree soluble sugars and starch declined in all organs as nut growth occurred. During the same time period, organs of "off" trees began to accumulate greater concentrations of soluble sugars and starch and exceeded concentrations measured in organs of "on" trees.**

California is the second largest producer of pistachio nuts in the world and accounts for 99% of all pistachio nuts produced in the United States. 'Kerman' pistachio is the most widely grown cultivar in California. Inflorescence buds are produced on current shoots, and ≈30% to 40% abscise on 'Kerman' pistachio trees with either a heavy crop ("on") or a light crop ("off") during an initial growth phase that coincides with the lignification of the endocarp (Crane and Iwakiri, 1981; Porlingis, 1974) from May to June in California. A more pronounced second phase of bud abscission accounting for an additional 50% bud drop occurs only on trees that are in a heavy cropping cycle and, as a result, these trees will be "off" the next year. This latter bud abscission coincides with rapid seed growth (Crane and Iwakiri, 1987), resulting in the undesirable biennial bearing of pistachio trees. The causes and mechanisms of inflorescence bud abscission in pistachio are poorly understood. The factors that determine, enhance, or limit inflorescence bud abscission need to be elucidated to control biennial bearing in pistachio.

Pistachio trees bear nuts on leafless 1-year-old wood, and anthesis occurs well before the development of a competent photosynthetic leaf area on current-year wood. The growth and development of nuts take place from early April through mid-September, whereas new vegetative shoots begin growing in late March to the middle of May (Crane, 1986; Crane et al., 1971). Inflorescence bud primordia for the following year's bloom are initiated and differentiated on current-year shoots during April and May, but bud growth continues until June (Crane, 1986; Takeda, 1980; Takeda et al., 1979). Inflorescence bud formation and abscission that results in alternate bearing among pistachio trees occurs during the year of the "on" crop. In contrast, other fruit trees differentiate fewer floral buds during the cropping year. Alternate bearing in pistachio has been correlated with 1) competition for resources, 2) influences of hormones derived from or diverted toward seed (Crane, 1971; Crane et al., 1973; Monselis and Goldschmidt, 1982; Porlingis, 1974; Takeda et al., 1980), 3) the amount of available leaf area (Crane et al., 1973; Porlingis, 1974), 4) the amount of available carbohydrates (Crane and Al-Shalan, 1977; Porlingis, 1974; Takeda et al., 1980), 5) the number of nuts on bearing wood, and 6) seed development (Crane et al., 1973; Crane and Iwakiri, 1987; Crane and Nelson, 1972; Porlingis, 1974; Wolpert and Ferguson, 1990).

In pistachio trees, stored carbohydrates and nitrogen are used with current-season photoassimilates to growth and to maintain reproductive and vegetative plant parts (Crane et al., 1976; Gifford and Evans, 1981; Goldschmidt and Golomb, 1982; Kozlowski, 1992; Newell, 1987; Roper et al., 1987; Scholefield et al., 1985), resulting in seasonal variations in concentrations of carbohydrates in different organs, which are similar to those found in other trees (Birrenkott et al., 1991; Goldschmidt and Golomb, 1982; Loescher et al., 1985; Oliveira and Priestly, 1988). The reproductive growth

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events influence patterns of resource allocation to favor reproductive organs in many plant species (Faust, 1989; Newell, 1987; Roper et al., 1988; Takeda et al., 1980). In pistachio, developing nuts may be the strongest sinks, as they have the greatest amounts of recently fixed $^{14}C$-photosynthates compared to other organs on the branch, which were tested (Takeda et al., 1980). Crane and Al-Shalan (1977) observed a rapid decline in concentrations of total sugars in bark and wood during flowering and growth of pistachio shoots and nuts as well as lower concentrations of starch in bark and wood in fruiting than defruited trees. On the other hand, Crane et al. (1976) did not find differences in concentrations of total sugars among current and 1-year-old wood of "on" and "off" pistachio trees.

Most of the investigations on pistachio and other fruit species that have reported the relationships between carbohydrate concentrations and the development of reproductive organs used fruiting versus defruited or deflorated trees (Crane and Al-Shalan, 1977; Crane et al., 1973, 1976; Kappel, 1991; Porlingis, 1974; Post and Stan, 1983; Roper et al., 1988; Stutte and Martin, 1986; Takeda et al., 1980). Thus, the "on" status was natural and the "off" status was artificial as a result of defruiting or deflorating the "on" trees. Furthermore, most of these investigations confined their studies to only current and 1-year-old wood, consequently failing to examine the dynamics of storage carbohydrates in other parts of the fruit trees, especially during natural cycles of heavy ("on") and light ("off") cropping. We contend that using trees that are defruited or deflorated establishes an artificial condition that makes carbohydrate comparison questionable. The most important feature in the understanding of pistachio reproductive biology is its contrast with other deciduous fruit species. In the latter, few floral buds are produced in the year of the heavy crop—the "on" year; in contrast, for pistachio, maximum floral bud production occurs in the heavy crop year; but, in May and June and again in August of that same year, massive floral bud abscission occurs. The crown of a pistachio tree consists of a collection of leafless branches (metamers) terminating in leafy, current-year shoots at the periphery of the crown. These new shoots bear pinnately compound leaves, each subtending a single inflorescence bud at their axils and a vegetative bud at the terminus. Nuts are borne on 1-year-old wood, whereas vegetative buds on current- and previous-year wood remain dormant because of the strong apical dominance of the terminal vegetative bud on the current shoot. For the study reported here, experimental trees were in their natural "on" and "off" bearing cycles and were sampled over 2 years.

In Nzima et al. (1997), we used pistachio trees in their natural bearing cycles and concluded the following when "on" trees were compared to "off" trees: 1) "on" tree leaves were greater in number, expanded faster in the first 30 d of growth but were smaller at maturity; 2) "on" tree leaf area was greater because of more leaves; 3) 85% inflorescence bud abscission occurred from "on" tree shoots, whereas 35% inflorescence bud abscission from "off" tree shoots; 4) "on" tree inflorescence buds were 30% lighter in dry mass; 5) "on" trees had greater total dry mass; and 6) the demands of fruiting in "on" trees resulted in greater dry mass loss from leaves, 1-year-old wood, and inflorescence buds by the end of the growing season.

In this paper we tested these two hypotheses.

1) Carbohydrate concentration early in the growing season is greater in organs examined from "on" than "off" trees. This hypothesis presumes the rapid growth and large population of floral buds stems from high initial carbohydrate concentrations.
2) Carbohydrate concentration remains high in all "on" tree organs except inflorescence buds as the major waves of inflorescence bud and nut abscission take place.

## Materials and Methods

**Experimental trees.** In 1990, most of the *Pistachio vera* 'Kerman' on *Pistacia atlantica* Desf. rootstock trees at the Wolfskill Experimental Orchard, Winters, Calif., produced an "on" crop of 40 to 50 kg/tree of dry nuts, while "off" trees produced 5 to 12 kg/tree. Eight trees were selected for uniform size, crop load, canopy size, and leaf color and were paired based on their crop loads, such that four trees were naturally "on" and the other four were naturally "off". Trees in the orchard were spaced 6.1 m between and along the rows and were sampled in 1991 and 1992 as they passed through natural "on" and "off" cycles. Mature trees can range from several tons of nuts per hectare in the "on" year to a few hundred kilograms of nuts per hectare in the "off" year. Each of the eight trees had three primary scaffold branches arising from the main scion trunk. Standard commercial practices for weed control, fertilizer application, and irrigation scheduling for the trees were followed during the experiment.

**Plant sampling.** Samples for chemical analysis were taken from "on" and "off" trees in 1991 and from "on" and "off" trees in 1992 between 1000 and 1400 HR on each date and included the following: 1) from each of the four "on" and "off" trees bark, wood, leaves, inflorescence buds, rachises, and nuts from six current and 1-year-old shoots; 2) bark and wood samples from three primary scaffold branches and three tertiary branches each subtended by one of the primary branches; and 3) three root samples from under the dripline. In 1991 samples were collected on 13 Apr. [full bloom + 10 d (FB + 10)], 2 June (FB + 60), 16 June (FB + 74), 20 July (FB + 108), 21 Aug. (FB + 140), and 19 Sept. (FB + 171). During 1992, samples were collected on 13 Apr. (FB + 10), 2 June (FB + 60), 18 June (FB + 76), 17 July (FB + 105), 29 Aug. (FB + 148), and 10 Sept. (FB + 160). These dates were chosen to coincide with vegetative growth (March to May), increase in pericarp mass (April to May), lignification of the endocarp (May to June), and seed growth and development (late June to August). The last four sampling dates each year were not done on the same day after FB due to the number of samples (>3200) to be processed. As such, data for "off" trees in 1991 and 1992 are presented using the sampling dates for 1991, because most pistachio trees were "off" during 1991. Similarly, data for "on" trees in 1991 and 1992 are presented using 1992 sampling dates, when most pistachio trees had a heavy crop of nuts ("on"). Data presented here are the combined averages ±standard errors of each year for "on" and "off" trees.

Bark samples from the tertiary and primary scaffold branches were removed using a 15-mm-diameter circular saw. Wood samples were taken immediately from the same positions as the bark using a 9.5-mm drill bit. Roots, ≤10 mm in diameter, were collected from each hole (15 cm in diameter and 50 cm deep) within the tree dripline. All samples were kept in a large ice box and brought into the laboratory where they were stored at –30 °C before freeze drying in a drier (model 20 SRC-X; Virtis Co., Inc. New York).

**Carbohydrate extraction.** Two factors determined our sample handling scheme for carbohydrate analysis. The first was the similar leaf area expansion and dry matter accumulation among leaves, inflorescence buds, and current and 1-year-old wood of "on" or "off" trees in 1991 and 1992 (Nzima et al., 1997).

The second factor was that no significant difference was found in carbohydrate among "on" tree samples from 1991 and 1992 and among "off" tree samples from the same 2 years samples taken at FB + 10, FB + 60, or FB + 105, periods of vegetative growth, inflorescence bud abscission, and seed growth, respectively. Thus, for the 2 years of comparison, all carbohydrate analysis reported

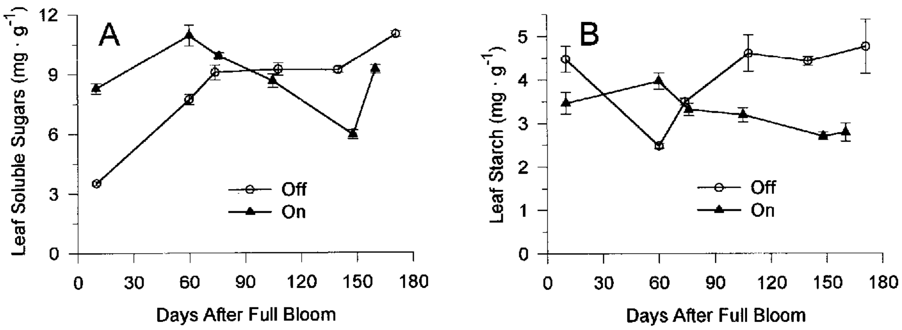


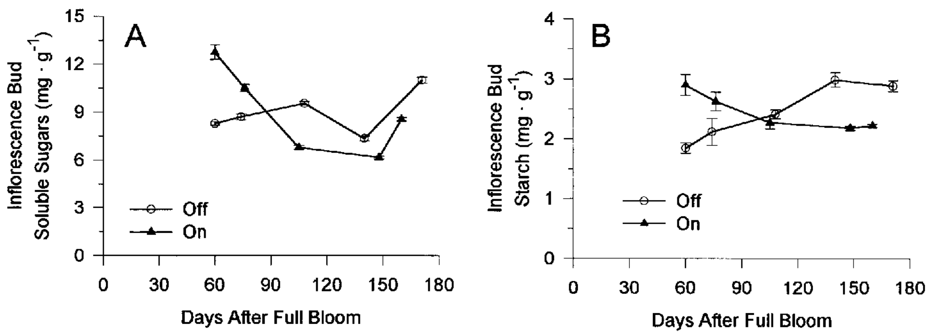
Fig. 1. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and of starch (**B**) in leaves of alternate bearing 'Kerman' pistachio trees. Data points are means and SES for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.

herein is from the 2 years of samples combined providing four sample trees for "on" and four sample trees for "off" trees. All samples were ground in a Thomas Wiley mill to pass through a 40-mesh screen.

The procedures for extracting soluble carbohydrates were modifications of published methods (Ettel, 1981; Smith, 1969; Stutte and Martin, 1986). Soluble sugars were extracted from each of two replicates for each organ sample for each of the four "on" and "off" trees. The 10-mg sample was added to 10 mL of 80% (v/v) methanol and homogenized for 20 s using a polytron (Brinkman Instruments, Westbury, N.Y.). The extraction was repeated three times, each time using 10 mL of the methanol. Homogenates were centrifuged for 5 min at maximum speed in a centrifuge (model CL; International Equipment Co., Needham, Mass.) and decanted, and the three 10-mL extracts were combined. The methanol was evaporated to 3 to 5 mL using a water bath at 80 °C, and then the volume was increased to 25 mL by adding deionized water. The methanol–water-soluble fractions were deproteinated using 2 mL each of 2% zinc sulfate and 2% barium hydroxide solutions (Newell, 1987) and then filtered through G6 fiberglass after the precipitate had settled. Extracts were diluted with 10 mL distilled water and stored in a freezer until immediately before determining the concentrations of glucose equivalents.

Residues after the methanol extraction were resuspended in 2 mL of 0.5 M NaOH and incubated for 45 min at 60 °C in a waterbath to hydrolyze starch. Once the suspensions were cool, their pHs were adjusted to ≈4.6 using 1 M HCl and 0.5 M NaOH. The volumes were made up to 5 mL with 0.2 M of sodium acetate-acetic acid buffer of pH 4.6 (Smith, 1969; Weier et al., 1977). Five hundred microliters of amyloglucosidase (EC 3.2.1.3) from *Rhizopus* mold (Lot 118F0330; Sigma Chemical Co., St. Louis) was added to each suspension, mixed, and incubated for 15 h at 45 °C in a waterbath to break starch chains into glucose units. The suspensions were centrifuged, the supernatant was collected, and their volumes were made up to 5 mL with 0.2 M of sodium acetate–acetic acid buffer. Starch extracts were deproteinated with 0.5 mL each of equimolar zinc sulfate and barium hydroxide solutions, filtered, and stored in a freezer.

Fig. 2. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and starch (**B**) in inflorescence buds of 'Kerman' pistachio trees. Data points are means and SES for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.



**SUGAR DETERMINATION.** Sucrose is the predominant sugar in bark and wood of pistachio trees followed in order by fructose, glucose, and inositol (Crane et al., 1976). Glucose equivalents of the methanol–water-soluble carbohydrates and starch glucose were used to determine concentrations using the anthrone method (Dowler and King, 1966; Yoshida et al., 1972). Ten milliliters of 2 g of anthrone reagent (Lot 49F0018; Sigma Chemical Co.) in 1 L of concentrated sulfuric acid were mixed with 5 mL of plant extract and heated for 10 min in boiling water. The solutions were cooled in ice for 10 min and assayed for glucose equivalents by measuring absorptance at 630 nm using a dipping probe colorimeter (PC 800; Brinkman Instruments, Westbury, N.Y.) with an acid-resistant Lexan plastic tip. Assays were all read within 40 min after boiling. Anthrone and glucose standard solutions were freshly prepared every assay day. Glucose equivalents were calculated from glucose standard curves, and the concentration of starch was obtained by multiplying the concentrations of the starch glucose equivalents by 0.9 (Dowler and King, 1966; Ettel, 1981; Yoshida et al., 1972). All concentrations were expressed on a dry mass basis.

**DATA ANALYSIS.** The concentrations of soluble sugars and starch in various organs were made across time. A repeated-measures analysis of variance (ANOVA) and MANOVA were performed using the General Linear Models procedure of SAS (SAS Institute, Cary, N.C.).

## Results

**EFFECT OF ALTERNATE BEARING ON LEAF NONSTRUCTURAL CARBOHYDRATES.** Leaves of "on" trees had twice the concentration (dry mass basis) of soluble sugars (8.3 ± 0.3 mg·g$^{-1}$) as those of "off" trees (3.5 ± 0.1 mg·g$^{-1}$) at FB + 10 (Fig. 1A). Concentrations of soluble sugars in leaves of "on" and "off" trees increased by FB + 60. Thereafter, "off" leaves contained greater soluble sugar concentration than "on" leaves. The starch concentrations of "on" tree leaves declined after FB + 60, whereas "off" leaf starch increased after FB + 60 and attained about twice the concentration of "on" leaves by the final sampling (Fig. 1B).

**EFFECTS OF ALTERNATE BEARING ON NONSTRUCTURAL CARBOHYDRATES OF INFLORESCENCE BUDS.** At FB + 60, inflorescence buds of "on" trees had concentrations of soluble sugars that were 54% (12.7 ± 0.5 vs. 8.3 ± 0.1 mg·g$^{-1}$) and starch that were 56% (2.9 ± 0.2 vs. 1.9 ± 0.1 mg·g$^{-1}$) greater than those of "off" trees (Fig. 2 A and B). After FB + 60 concentrations of soluble sugars and starch declined sharply in inflorescence buds of "on" trees (Fig. 2 A and B). Gener-

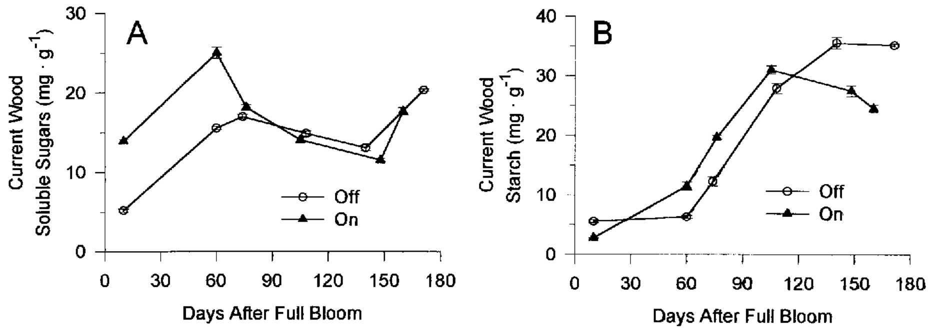


Fig. 3. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and starch (**B**) among individual current wood of 'Kerman' pistachio trees. Data points are means and SEs for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.

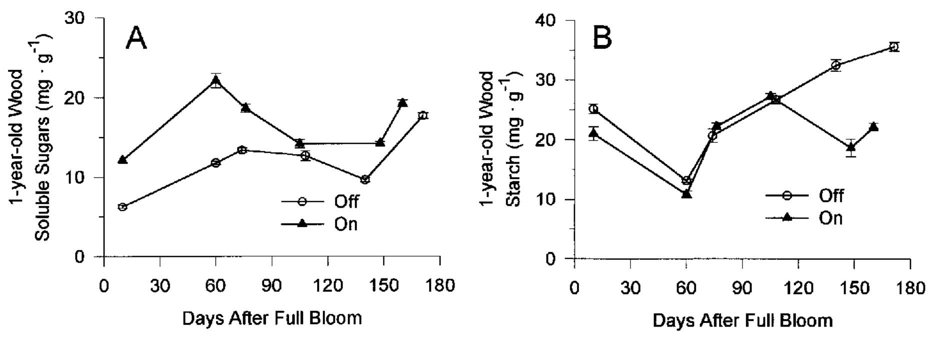
ally, concentrations of soluble sugars and starch increased throughout the season among inflorescence buds of "off" trees. By the last sampling dates (Fig. 2 A and B), inflorescence buds of "off" trees had 29% greater concentrations of soluble sugars (11.0 ± 0.2 vs. 8.6 ± 0.1 mg·g$^{-1}$) and 30% greater concentrations of starch (2.9 ± 0.1 vs. 2.2 ± 0.03 mg·g$^{-1}$) than buds of "on" trees.

**Effects of alternate bearing on nonstructural carbohydrates of current wood.** Current wood of "on" trees had twice the concentration of soluble sugars than "off" trees before FB + 60; thereafter, the concentrations of soluble sugars decreased in current wood of "on" and "off" trees before increasing again after FB + 140 (Fig. 3A). Between FB + 60 and FB + 108, starch concentration more than doubled for "on" and "off" trees; thereafter, "on" tree starch declined, whereas starch in "off" trees, leveled at 10 mg·g$^{-1}$ greater concentration than "on" trees (Fig 3B).

**Effects of alternate bearing on nonstructural carbohydrates of 1-year-old wood.** Concentrations of soluble sugars in 1-year-old wood of "on" trees declined from 22.1 ± 0.9 to ≈14.2 ± 0.2 mg·g$^{-1}$ between FB + 60 and FB + 148 (Fig. 4A). At each sampling date, soluble sugar concentrations in 1-year-old wood of "on" trees remained greater than those of "off" trees. Starch concentrations in 1-year-old wood of "on" and "off" trees were similar until about FB + 105 when the concentration in 1-year-old wood of "on" trees declined and that of "off" trees continued to increase (Fig. 4B).

**Effects of alternate bearing on nonstructural carbohydrates in primary scaffold branches.** Concentrations of soluble sugars were greater in primary scaffold branches of "on" trees until about FB + 108 when concentrations were similar in "on" and "off" trees (Fig. 5A). By the final sampling date, more soluble sugars were found in the "off" than in the "on" tree primary scaffold branches. Starch concentration declined among primary scaffold branches of "off" trees between FB + 10 and FB + 60; by the last sampling date, starch concentration more than doubled (Fig. 5B). In contrast, starch concentration decreased among primary scaffold branches of "on" trees between FB + 60 and the final sampling date (Fig. 5B).

Fig. 4. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and of starch (**B**) in 1-year-old wood of 'Kerman' pistachio trees. Data points are means and SEs for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.



**Effects of alternate bearing on nonstructural carbohydrates in tertiary branches.** Concentrations of soluble sugars in tertiary branches of "on" and "off" trees increased gradually throughout the season, remaining significantly greater in branches of "on" trees until the last sampling date when soluble sugar was in greater concentration in the "off" trees (Fig. 6A). During the growing season, starch concentration declined steadily by 32%, from 7.7 ± 0.4 to 5.3 ± 0.1 mg·g$^{-1}$ among tertiary branches of "on" trees while, starting at FB + 60, increasing by 139% (7.9 ± 0.3 to 18.9 ± 0.3 mg·g$^{-1}$) among branches of "off" trees by the time of the last sampling date (Fig. 6B).

**Effects of alternate bearing on nonstructural carbohydrates in roots.** Roots of "on" trees had greater concentrations of soluble sugars than those of "off" trees from FB + 10 to about FB + 76 and thereafter soluble sugar concentrations of "on" and "off" trees were similar (Fig. 7A). Starch concentrations were greater in roots of "on" trees at FB + 10, and by FB + 60 starch concentration was similar in "on" and "off" trees. Both declined in starch at about FB + 105, increasing thereafter to greater concentration in "off" than "on" trees by the final sampling date (Fig. 7B).

**Nonstructural carbohydrates in rachises and nuts from "on" trees.** The concentration of soluble sugars in rachises was fairly constant averaging ≈11.1 ± 0.7 mg·g$^{-1}$ throughout the fruiting season. In contrast, starch concentration increased threefold between about FB + 60 and FB + 105 (from 3.4 ± 0.1 to 9.4 ± 0.8 mg·g$^{-1}$) before declining to 3.6 ± 0.2 mg·g$^{-1}$ toward harvest (Fig. 8A).

Developing nuts averaged 7.7 ± 0.5 mg·g$^{-1}$ of soluble sugars until after FB + 76, when the soluble sugar concentration increased sharply by about FB + 105, then declining to 17.1 ± 0.9 mg·g$^{-1}$ by FB + 160 (Fig. 8B). In contrast, starch concentration in developing nuts ranged from 2.8 ± 0.1 to 5.9 ± 0.3 mg·g$^{-1}$ during the season.

## Discussion

There is common agreement that initial growth and development of reproductive and vegetative organs of deciduous tree species derive considerable proportions of the carbohydrate requirements from stored reserves (Dickson, 1989; Ferree and Palmer, 1982; Kozlowski, 1992; Loescher et al., 1985, 1990) because anthesis and fruit set precede the development of a competent photosynthetic system. The use of stored reserves by alternate-bearing pistachio is unique because this involves vegetative growth during the "off" year and also includes the growth of fruit and nuts and the initiation and development of inflorescence buds in the "on" year. Leaves of "on"

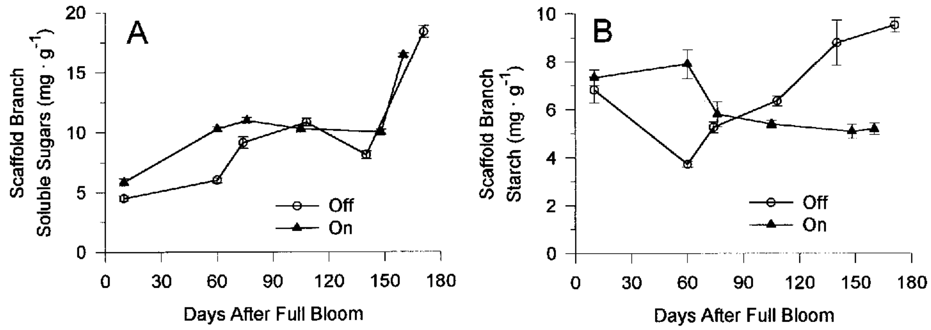
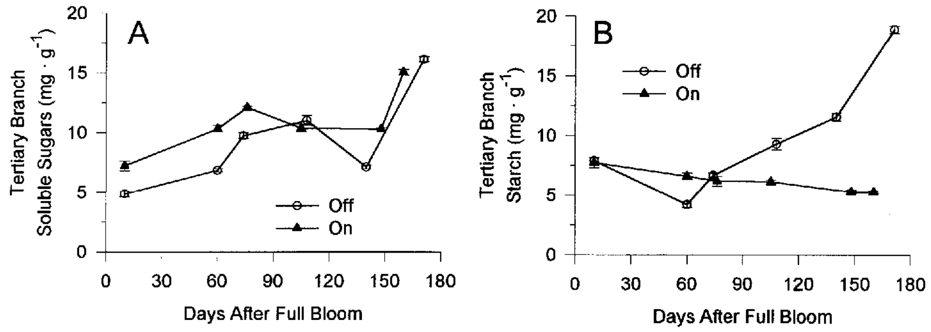


Fig. 5. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and starch (**B**) among individual scaffold branches of 'Kerman' pistachio trees. Data points are means and SEs for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.

pistachio trees accumulated soluble sugars and starch during the first 60 d after FB, whereas those of "off" trees accumulated only soluble sugars (Fig. 1 A and B). Sixty percent of pistachio nuts had abscised by FB + 30, and an additional 25% abscised during the subsequent 30 d (Nzima et al., 1997), coincident with accumulation of carbohydrates in leaves of "on" trees. Fruit set and flower abscission have been associated with competition for resources among fruitlets and between reproductive and vegetative organs in other fruit species (Byers et al., 1991; Farrington and Pate, 1981; Lloyd, 1980; Newell, 1987; Stephenson, 1983). At the early sampling dates each year (FB + 10 and FB + 60), "on" trees had higher concentrations of soluble sugar than "off" trees in leaves, inflorescence buds, current wood, 1-year-old wood, tertiary branches, scaffold branches, and roots. During the early development stage we have shown that leaf number and growth rate is greater in "on" than "off" trees (Nzima et al., 1997). Further, in that same work we reported that, as "on" tree nut growth occurred and particularly after FB + 76, greater dry mass loss was found in inflorescence buds, leaves, current wood, 1-year-old wood, and rachises. The combined carbohydrate reserves could support the early growth commitments of "on" trees but, between FB + 10 and FB + 60, the 85% nut abscission and 40% inflorescence bud abscission may have been caused by preferential soluble sugar transport to the developing leaf canopy and woody structure (Nzima et al., 1997) and Figs. 1–7A.

Carbohydrate concentrations in inflorescence buds of "on" trees decreased until nut maturity because the buds were either weak sinks (Takeda et al., 1980) or inefficient in using imported photosynthates. Inflorescence buds abscise equally from "on" and "off" trees during the first wave of bud abscission, whereas the second wave of bud abscission is confined to only "on" trees (Crane and Iwakiri, 1981, 1987; Nzima et al., 1997; Porlingis, 1974). Initially, inflorescence buds sampled from "off" trees had lower concentrations of carbohydrates than those of "on" trees; however, the inverse occurred after FB + 76 (Fig. 2). It is conceivable that low concentrations of carbohydrates in inflorescence buds may trigger the abscission process irrespective of when the low concentration occurs in the developmental sequence.

Fig. 6. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and starch (**B**) among tertiary scaffold branches of 'Kerman' pistachio trees. Data points are means and SEs for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.



Pistachio nut growth and development starts well before leaf photosynthetic competence and continues almost to harvest (Nzima et al., 1997). The pericarp increases rapidly in diameter and dry mass to its maximum size between May and June (about FB + 25 to FB + 90); then, the endocarp lignifies and seed growth follows from July to late August (about FB + 90 to FB + 150) (Crane et al., 1971). Our results suggest that developing nuts derive their carbon requirements from current photoassimilates and stored reserves. Concentrations of soluble sugars increased markedly in nuts concomitant with rapid decline in concentrations of both soluble sugars and starch in leaves (Fig. 1 A and B), inflorescence buds (Fig. 2 A and B), primary scaffold branches (Fig. 5 A and B), and tertiary branches (Fig. 6 A and B) between FB + 60 and FB + 148 (early June to late August). Starch concentrations in 1-year-old wood (Fig. 4B) and small roots (Fig. 7B) decreased markedly ≈16 d after decreases that were noted in the other organs mentioned above. Decreases in starch concentrations in current wood (Fig. 3B) and rachises (Fig. 8A) occurred ≈45 d after those in the other organs. In these comparisons, the decreases in starch concentrations coincided with increases in concentrations of soluble sugars in these organs, suggesting conversion of starch to soluble sugars for possible remobilization. In contrast to the heavily producing "on" trees, the "off" trees were accumulating starch in individual organs without having the demand of nut growth. Thus, the immense demand for carbohydrates by developing nuts establishes them as the major sink, whereas the other organs change roles between sinks and sources as the season progresses (Weinbaum et al., 1994). Shifts in sink–source relationships have been reported in many other plant species (Daie, 1985; Gifford and Evans, 1981; Hansen, 1989). Similarly, use of stored reserve carbohydrates simultaneously with current photosynthates for the growth and development of reproductive structures has been documented for apples (*Malus communis* Borkh.) (Byers et al., 1991; Ferree and Palmer, 1982; Oliviera and Priestly, 1988), sweet cherry (*Prunus avium* L.) (Loescher et al., 1985; Roper and Kennedy, 1986; Roper et al., 1988), *Phaseolus vulgaris* (Geiger and Shieh, 1988), *Citrus paradisi* McFady) (Garcia-Luis et al., 1988; Goldschmidt and Golomb, 1982), and pecan (*Carya illinoinensis* Wangeth.) (Marquard, 1987; Smith et al., 1986; Wood and McMeans, 1981).

As starch decreased in inflorescence buds (Fig. 2B), it increased in "on" current wood (Fig. 3B). Perhaps current wood was the second strongest sink to nuts on an individual branch. We found differences in the

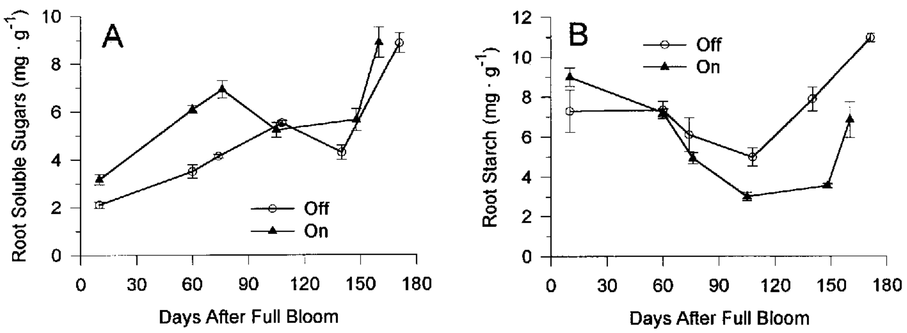
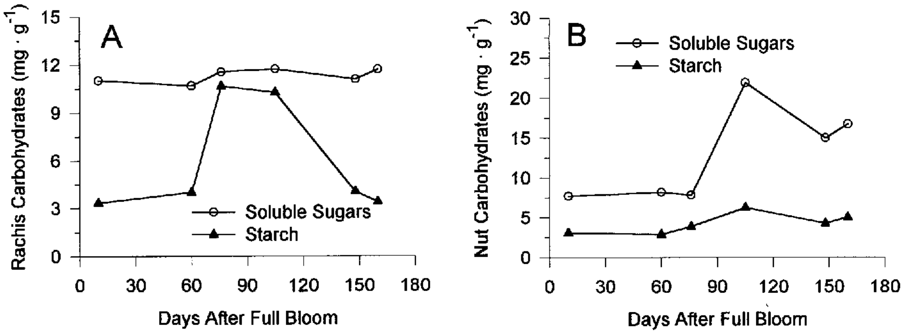


Fig. 7. Changes in concentrations (dry mass basis) of soluble sugars (**A**) and starch (**B**) in small roots (≤10 mm in diameter) of 'Kerman' pistachio trees. Data points are means and SES for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.

concentrations of soluble sugars in current wood from "on" and "off" trees until FB + 60 (April to June) and of starch in current wood after FB + 105 (mid-July). Crane et al. (1976) found no differences in soluble sugars and starch in current wood of "on" and "off" trees; this may be because they used defruited trees that had accumulated large quantities of starch during the "off" year. Several other independent studies found greater total amounts of carbohydrates in "off" than "on" tree species, including pistachio (Weinbaum et al., 1994), citrus (Monselise and Goldschmidt, 1982), and sweet cherry (Kappel, 1991; Keller and Loescher, 1989). However, Newell (1987) reported that remobilization of carbohydrates from other parts of a fruiting California buckeye (*Aesculus californica* Spach) tree maintained higher carbohydrate concentrations in reproductive organs of "on" than in "off" trees.

The pistachio tree either preferentially accumulates carbohydrates in shoot organs before restocking the root system or its root growth uses large quantities of carbohydrates during the "off" year, resulting in delays in accumulating carbohydrates in roots until July. Starch accumulation in roots of "off" trees began after FB + 105, which was ≈6 weeks earlier than starch accumulation in roots of "on" trees. In "off" trees, starch concentration in leaves, 1-year-old wood, tertiary and primary scaffold branches, and roots declined during spring, while starch concentrations accumulated in similar organs of "on" trees. The inverse occurred after FB + 60 (early June), except in current and 1-year-old wood in which there were delays of 2 to 6 weeks before starch concentration increased (Figs. 3B and 4B).

Fig. 8. Changes in concentrations (dry mass basis) of nonstructural carbohydrates in rachises (**A**) and nuts (**B**) of "on" 'Kerman' pistachio trees. Data points are means and SES for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on" in 1992.



In conclusion we submit the following.

1) "On" pistachio trees enter the growing season with a higher concentration of reserve soluble sugar and starch than do "off" trees.

2) In "on" trees the early carbohydrate demands of the greater number of leaves and their more rapid growth rate, plus developing nuts, and inflorescence buds exceeds that of "off" trees.

3) "Off" tree inflorescence buds contained far greater concentration of soluble sugar and starch than "on" buds by the end of the growing season.

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