Seasonal carbohydrate storage and mobilization in bearing and non-bearing pistachio (*Pistacia vera*) trees

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Summary We analyzed annual carbohydrate storage and mobilization of bearing ("on") and non-bearing ("off") 'Kerman' pistachio (*Pistacia vera* L.) trees growing on three different rootstocks. On all rootstocks, carbohydrate storage in shoots and branches of "on" and "off" trees was lowest following the spring growth flush. In "off" trees, stored carbohydrates increased and remained high after the initial growth flush. In "on" trees, stem carbohydrates increased temporarily in early summer, but were mobilized in mid-season during kernel fill, and then increased again after nut harvest. During the dormant season, the only substantial differences in carbohydrate storage between previously "on" and "off" trees were found in the roots of the weakest rootstock. The annual carbohydrate storage and mobilization pattern in canopy branches of heavily cropped pistachio trees appeared to be driven by carbohydrate demands related to nut development and untempered by tree vigor. 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 inflorescence bud abscission. Thus, the alternate bearing pattern associated with inflorescence bud abscission in 'Kerman' pistachio may be a function of mid-season mobilization of stored carbohydrates in current-season stems resulting in stimulation of inflorescence bud abscission.

Keywords: alternate bearing, carbohydrate concentration, carbohydrate content, carbon partitioning, dry mass accumulation.

Introduction

Annual patterns of carbohydrate storage and mobilization vary among species and genotypes based on growing conditions, growth characteristics, crop load and other factors. Generally, carbohydrate reserves of stems and branches of temperate deciduous trees decrease during the spring growth flush, reach a minimum during early summer, and subsequently increase to a maximum during late summer and early autumn, before the onset of dormancy (Kozlowski and Keller 1966, Kramer and Kozlowski 1979, Oliveira and Priestly 1988, Kozlowski 1992).

In many tropical, subtropical and evergreen species, carbohydrate storage and mobilization patterns differ from those in temperate deciduous trees. For example, in macadamia (*Macadamia integrifolia* Maiden & Betche), carbohydrate storage fluctuates rhythmically with growth flushes, and reproductive growth is heavily dependent on carbohydrate reserves (Cormack and Bate 1976, Stephenson et al. 1989*a*, 1989*b*). Coffee (*Coffea arabica* L.) fruit are dependent on both current photosynthates and reserve carbohydrates as evidenced by an accumulation of reserves after the spring flush followed by a depletion of reserves during fruit development (Wormer and Ebagole 1965, Patel 1970).

The annual pattern of carbohydrate storage and mobilization in pistachio (*Pistacia vera* L.) is of interest, in relation to the alternate bearing cycle. Crane and Al-Shalan (1977) determined annual starch and sugar concentrations for 1-year-old wood of bearing ("on") and non-bearing ("off") 40-year-old 'Bronte' pistachio trees in 1970 and 1971 and found slight differences between "on" and "off" trees in 1970 but not in 1971. The most complete analysis of carbohydrate storage patterns in pistachio was reported by Nzima et al. (1997*a*) who followed eight 'Kerman' pistachio trees on *P. atlantica* Desf. rootstock for two years (one alternate bearing cycle), and presented data from bloom to harvest each year. Their data showed an increase in starch and soluble sugar concentrations in current-season and 1-year-old stems immediately following bloom in both "on" and "off" trees, and then a marked decline in "on" trees about 100 days after bloom, coincident with the kernel development stage of nut growth. This pattern is similar to that reported for macadamia nut and coffee (Wormer and Ebagole 1965, Patel 1970, Cormack and Bate 1976, Stephenson et al. 1989*a*, 1989*b*) but is not typical of the pattern observed in temperate deciduous trees. Furthermore, Nzima et al. (1997*a*) showed a slight increase in soluble sugar and starch concentrations in current-season and 1-year-old stems of "on" trees following nut maturity. Rosecrance et al. (1998) and Weinbaum et al. (1994) reported significantly

lower starch concentrations in canopy branches during the dormant season following an "on" year compared with an "off" year, suggesting that the slight post-harvest increase in concentration shown by Nzima et al. (1997*a*) may have no significance for overall storage reserves. All of these studies were conducted on 'Kerman' trees grafted on *P. atlantica* rootstock, which is the least vigorous rootstock used for pistachio production in California. Most new commercial plantings of pistachio are grafted on either *P. integerrima* Stew. selection Pioneer Gold I (PGI) or *P. atlantica* × *P. integerrima* selection UC Berkeley I (UCB) rootstocks. Both of these rootstocks produce more vigorous trees than the *P. atlantica* rootstock (Spann et al. 2007). It is not known whether these reported patterns in carbohydrate storage and in-season mobilization are a function of rootstock or tree vigor, or both.

The objectives of our study were to: (1) compare the annual carbohydrate storage patterns of "on" and "off" pistachio trees on the three common rootstocks used in Californian pistachio production; and (2) verify that carbohydrates stored during the lag phase of nut development (Stage II), when supply presumably exceeds demand, are mobilized later in the same season during the kernel-fill stage (Stage III) of pistachio nut development, unlike most other temperate deciduous trees.

Materials and methods

All experiments were conducted in a rootstock trial at the University of California, Kearney Agricultural Center, Parlier, CA, (36°36′42″ N, 119°31′34″ W, 103.6 m a.s.l.). The trial was planted in February 1989 with 1-year-old nursery-grown seedlings that were field budded to *P. vera* cultivar 'Kerman' after planting. There were 20 rows of 18 trees spaced 5 m apart within rows and 6 m between rows. The trees were planted in a randomized complete block design (RCBD) with 90 blocks; each block spanned four rows and contained one tree of each of four rootstocks. Before the trial, the trees had received standard horticultural care typical of commercial production, including dormant pruning, irrigation, fertilization and pest control.

The current experiment was a completely randomized design overlaying the original RCBD. The original planting consisted of trees on four rootstocks, however, we limited our study to trees on the three rootstocks currently used commercially in California: *P. atlantica* (Atl), *P. integerrima* Stew. selection Pioneer Gold I (PGI) and *P. atlantica* × *P. integerrima* selection UC Berkeley I (UCB).

During spring of 2002, eight trees on each of the three rootstocks were selected for uniformity within a rootstock from within eight contiguous rows of the block. Based on the bearing history of this block, 2002 was considered an "on" year. Four of the trees on each rootstock were randomly selected, and the immature rachises were removed on June 10 to produce "off" trees in an otherwise "on" year. Aside from this manipulation, the trees were treated similarly and managed according to standard commercial practices. No data were collected in 2002 following the crop load manipulation.

The trees that were "on" in 2002 had a light "off" crop in 2003. These trees were made completely "off," to maximize the difference between treatments, by removing the immature rachises by hand on April 25, 2003 (~1 week after bloom). The trees that had been "off" in 2002 were allowed to bear normally in 2003. These manipulations allowed for the study of tree carbohydrate partitioning and storage within "on" and "off" trees in the same year (2003), eliminating year-to-year environmental variation.

Beginning January 22, 2003 and continuing at regular intervals throughout the season, two similar stems (one from the north and one from the south side of the tree) were collected from a peripheral mid-height position in the canopy of each "on" and "off" tree on each rootstock. The sampled stems, which comprised current-season (2003), 1-year-old (2002) and 2-year-old (2001) growth, were immediately placed on ice and taken to a laboratory. In the laboratory, the stem tissue was separated by age, leaves were removed from the current-season tissue and any nut bearing rachises were removed from the 1-year-old wood, and the nuts were separated from the rachises and counted. The length of each stem segment (current-season, 1-year-old and 2-year-old) was measured and the number of nodes counted. All tissues were dried to a constant mass at 60 °C, weighed, ground to pass a 40-mesh (0.60 mm) screen and analyzed for total nonstructural carbohydrate (TNC) by standard methods (Smith 1969) at the Division of Agriculture and Natural Resources Analytical Lab at the University of California, Davis, CA (ANR Analytical Lab 2006). Starch was hydrolyzed with amyloglucosidase, and glucose, sucrose and fructose were analyzed by HPLC with a fast carbohydrate column (HPAP, Bio-Rad Laboratories, Hercules, CA). Concentrations were expressed as glucose equivalents per gram dry mass of tissue (mg g^{-1}). Concentrations of glucose, sucrose and fructose were summed to give an estimate of TNC.

On January 22, May 7, July 16 and August 27, 2003, root, trunk wood and bark samples were collected from each of the four "on" and "off" trees on each rootstock. Sampled roots were about 4–6 mm in diameter, and two 6–8 cm sections were collected from within the drip line of each tree at a depth of ~20 cm. Trunk and bark samples were collected with a power drill fitted with a 1-cm-diameter plug-cutting bit. Two plugs were cut from the trunk of each tree, above the graft union, to a depth of ~1.2 cm, and the bark (~3 mm thick) was separated from the underlying wood of each plug. Bark, trunk wood and washed roots were dried, ground and analyzed as described for the stem tissues.

The carbohydrate data collected in 2003 for the different tissue samples were subject to a repeated measures analysis of variance. Tukey's adjustment was used to adjust *P*-values to compensate for the large number of analyses performed. Significance is reported at $P = 0.05$.

Results

Rates of accumulation of nut dry mass and stem dry mass per unit length were similar for the three rootstocks, but there were clear differences in the latter between "on" and "off" trees

(Figure 1). The rate of increase in dry mass per unit length in current-season stems was similar for "on" and "off" trees on all rootstocks through early May (Figure 1). However, concomitant with the start of nut dry mass gain in early May, "on" stems had a lower rate of dry mass gain per unit length than "off" stems across rootstocks. Within each rootstock, stem dry mass gain continued to occur at a relatively steady rate through nut maturity (late August) for stems from both "on" and "off" trees. Little stem dry mass accumulation occurred after nut maturity/harvest.

Nut dry mass growth rates did not differ significantly across rootstocks (Figure 1) so the data from the three rootstocks were pooled (Figure 2). The rate of nut dry mass accumulation varied with nut development stage and increased rapidly to 0.013 g day^{-1} in early May (Figure 2) when the hull (mesocarp) and shell (endocarp) were rapidly expanding. Nut dry mass accumulation rate steadily declined during June to a low of 0.007 g day^{-1}; this was the period of nut development when expansion stopped and shell lignification occurred. During early July, nut dry mass accumulation increased rapidly to 0.015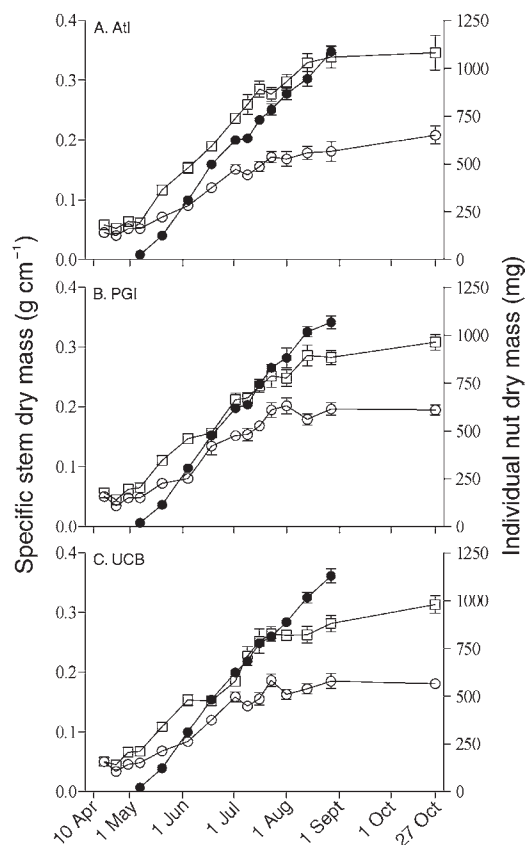 g day^{-1} and remained relatively high during July. This coincided with the period of rapid embryo growth, i.e., kernel fill. Dry mass accumulation rates declined during August as kernel fill was completed and final nut ripening occurred.

Temporal patterns of carbohydrate storage and mobilization in vegetative tissues varied with crop load over the season (Tables 1 and 2). Rootstock had no significant effect on these patterns in any of the tissues except for roots at the January sampling date when "off" trees on Atl had significantly lower TNC concentration than "off" trees on PGI (110.0 versus 177.0 mg g$_{DM}^{-1}$, respectively), resulting in a significant rootstock × crop load interaction (Table 2, Figure 3C). Regardless of rootstock or previous-year bearing status, all trees started the season with similar concentrations of carbohydrates in 1- and 2-year-old stems (Figures 4B and 4C). The TNC concentration in bark tissue was relatively low compared with other tissues during the dormant season (e.g., January 22), and there were no significant differences between trees at this time (Figure 3A). As in bark tissue, TNC concentrations in dormant trunk wood did not differ significantly between trees on January 22, but TNC concentrations in trunk wood were considerably higher than in bark (Figure 3B). Although, on January 22, there was a significant difference in root TNC concentration between "off" trees on Atl, the least vigorous rootstock, and "off" trees on PGI, the most vigorous rootstock, there were no differences between "on" and "off" trees within a rootstock at that time (Figure 3C).

Stored carbohydrates in 1- and 2-year-old segments of stems of both "on" and "off" trees declined steadily in the period before bloom and vegetative bud break (January 22– April 9; Figures 4B and 4C). During this period, carbohydrate concentrations in all 1- and 2-year-old segments from trees on each rootstock declined at a similar rate, such that there were no significant differences between trees on April 9. During the same period, bark, trunk wood and root TNC concentrations decreased at similar rates in "on" and "off" trees and across rootstocks, and there were no significant differences between trees on May 7 (Figures 3A–C).

Figure 1. Stem dry mass per unit length of current-season stems from "on" (○) and "off" (□) 'Kerman' pistachio trees on three rootstocks and mean individual nut dry mass for the nuts subtending current-season stems from "on" trees (●). Error bars are 1 SE. Rootstocks: (A) Atl, *Pistacia atlantica*; (B) PGI, *P. integerrima* selection Pioneer Gold I; and (C) UCB, *P. atlantica* × *P. integerrima* selection University of California Berkeley I.
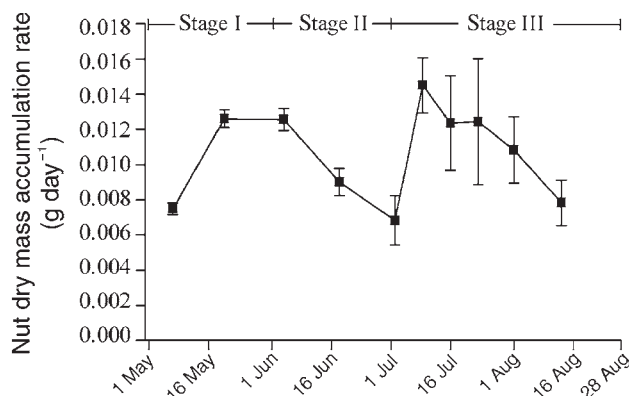

Figure 2. Pistachio nut dry mass accumulation rate during 2003. Error bars are 1 SE. Nut development stages are indicated across the top. Data were not significantly different among trees on different rootstocks, so data are pooled values of samples across rootstocks.

Table 1. Results of repeated measures analysis of variance of total nonstructural carbohydrate concentration for current-season and 1- and 2-year-old stems of mature 'Kerman' pistachio trees on three rootstocks with two crop loads. Abbreviations: Num df and Den df, numerator and denominator degrees of freedom, respectively.

Effect	Num df	Den df	F	P
Current-season stems				
Rootstock (Rs)	2	18	0.03	0.9695
Crop load (Crop)	1	18	14.35	0.0013
Rs × Crop	2	18	0.14	0.8706
Time	3	53	434.72	< 0.0001
Rs × Time	6	53	1.19	0.3245
Crop × Time	3	53	18.95	< 0.0001
Rs × Crop × Time	6	53	0.98	0.4512
1-year-old stems				
Rs	2	18	2.31	0.1279
Crop	1	18	60.67	< 0.0001
Rs × Crop	2	18	0.30	0.7430
Time	5	72	91.42	< 0.0001
Rs × Time	10	72	1.31	0.2423
Crop × Time	5	72	32.81	< 0.0001
Rs × Crop × Time	10	72	0.95	0.4967
2-year-old stems				
Rs	2	18	0.49	0.6200
Crop	1	18	27.02	< 0.0001
Rs × Crop	2	18	0.14	0.8688
Time	5	74	68.25	< 0.0001
Rs × Time	10	74	1.41	0.1944
Crop × Time	5	74	24.37	< 0.0001
Rs × Crop × Time	10	74	1.00	0.4551

Table 2. Results of repeated measures analysis of variance of total nonstructural carbohydrate concentration for bark, trunk wood and roots of mature 'Kerman' pistachio trees on three rootstocks with two crop loads. Abbreviations: Num df and Den df, numerator and denominator degrees of freedom, respectively.

Effect	Num df	Den df	F	P
Bark				
Rootstock (Rs)	2	18	1.23	0.3166
Crop load (Crop)	1	18	6.24	0.0224
Rs × Crop	2	18	0.35	0.7123
Time	3	41	121.18	< 0.0001
Rs × Time	6	41	2.44	0.0414
Crop × Time	3	41	1.51	0.2261
Rs × Crop × Time	6	41	1.98	0.0912
Trunk wood				
Rs	2	18	0.60	0.5570
Crop	1	18	6.68	0.0187
Rs × Crop	2	18	0.04	0.9638
Time	3	42	72.51	< 0.0001
Rs × Time	6	42	1.09	0.3854
Crop × Time	3	42	9.85	< 0.0001
Rs × Crop × Time	6	42	1.78	0.1268
Roots				
Rs	2	18	2.97	0.0766
Crop	1	18	20.30	0.0003
Rs × Crop	2	18	4.87	0.0204
Time	3	40	57.70	< 0.0001
Rs × Time	6	40	1.86	0.1111
Crop × Time	3	40	5.40	0.0032
Rs × Crop × Time	6	40	1.83	0.1175

After bloom and vegetative bud break (April 9), TNC concentrations in 1- and 2-year-old segments declined slightly more rapidly in "on" trees than in "off" trees across all rootstocks; however, this resulted in no significant difference between "on" and "off" trees on June 4 (Figures 4B and 4C).

Following the completion of the spring growth flush and Stage I of nut development (June 4; Figure 2), TNC concentration increased dramatically in all ages of stem tissue as well as in trunk wood of "on" and "off" trees on all rootstocks (Figures 3B and 4). These increases were coincident with Stage II of nut development when the dry mass accumulation of the fruit decreased by nearly 50% compared with Stage I (Figure 2). Following the end of Stage II (July 1), stems of all ages had similar TNC concentration across rootstocks and crop load (July 16; Figure 4). Concentrations of TNC in bark, trunk wood and roots were also similar across rootstocks and crop load at the end of Stage II (July 16; Figure 5).

Coincident with the onset of Stage III of nut growth, a period of rapid kernel development (about July 9; Figure 2), there were marked decreases in TNC concentrations in current-season, 1-year-old and 2-year-old stems (Figure 4), resulting in "on" trees on all rootstocks having significantly lower TNC concentrations than "off" trees on August 27 (Figure 4). Similarly, the decline in TNC concentration in trunk wood and roots of "on" trees during Stage III resulted in "on"

trees having significantly lower TNC concentrations on August 27 compared with "off" trees across all rootstocks (Figures 3B and 3C).

After the end of Stage III (August 27) and harvest, "on" trees stored carbohydrates rapidly in stem tissue (Figure 4). This rapid storage by "on" trees during the post-harvest period resulted in similar mean TNC concentrations for stems of a specific age across rootstocks and crop load at the end of the season (October 27).

Discussion

Seasonal patterns of nut dry mass accumulation were similar to those in pistachios grown in other parts of the San Joaquin Valley of California (Goldhamer and Beede 2004). Rates of stem dry mass accumulation per unit length for the three rootstocks were similar to the rates reported by Nzima et al. (1997*b*) for 25-year-old trees on Atl rootstock grown in the Sacramento Valley of California. Rate of stem dry mass growth per unit length and seasonal carbohydrate storage and mobilization varied with crop load but were fairly consistent across the three rootstocks even though trees on Atl rootstock are much less vigorous than trees on UCB and PGI rootstocks (Ferguson et al. 2005, Spann et al. 2007). These data support the concept that dry mass accumulation per unit length of
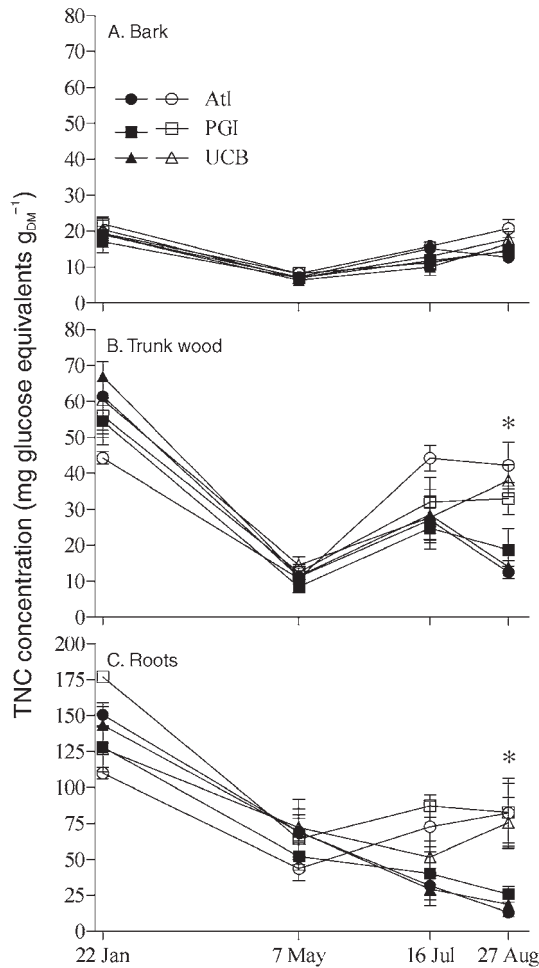
Figure 3. Annual changes in total nonstructural carbohydrate (TNC) concentration for (A) bark, (B) trunk wood and (C) roots of "on" (closed symbols) and "off" (open symbols) 'Kerman' pistachio trees on three rootstocks in 2003. Error bars are 1 SE. An asterisk (*) indicates significant differences between "on" and "off" trees across rootstocks, $P = 0.05$. Rootstocks: Atl, *Pistacia atlantica*; PGI, *P. integerrima* selection Pioneer Gold I; and UCB, *P. atlantica × P. integerrima* selection University of California Berkeley I.
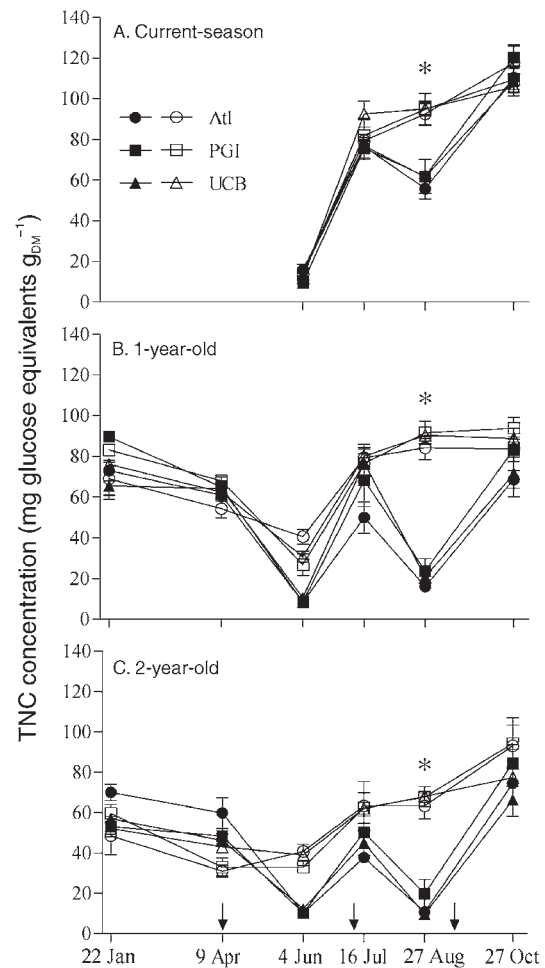
Figure 4. Annual changes in total nonstructural carbohydrate (TNC) concentration for (A) current season, (B) 1-year-old and (C) 2-year-old stems from "on" (closed symbols) and "off" (open symbols) 'Kerman' pistachio trees on three rootstocks in 2003. Error bars are 1 SE. Arrows indicate, from left to right, bud-break/bloom, onset of nut-fill and harvest. An asterisk (*) indicates significant differences between "on" and "off" trees across rootstocks, $P = 0.05$. Rootstocks: Atl, *Pistacia atlantica*; PGI, *P. integerrima* selection Pioneer Gold I; and UCB, *P. atlantica × P. integerrima* selection University of California Berkeley I.

young stems may have genetically determined optimal dimensions, achieved when resources are available but not when resources are lacking, as occurs when crop loads are heavy (Berman and DeJong 2003).

Although the patterns of nut dry mass accumulation in Figure 2 appear to be about linear across the season, the data do not reflect the rather unusual pattern of fruit growth of this species. The pistachio nuts grew quickly following pollination (mid-April) and reached full size by the end of May; however, at this point, only the shell (endocarp) and fleshy hull (mesocarp) were developed. Following this first phase of nut development, there was a marked decrease in growth rate (Figure 2). Starting in early July, there was a second period of rapid growth lasting about 6 weeks during which the kernel (seed = embryo and cotyledons) developed. This phase was marked by a doubling in dry mass gain per day (Figure 2). This general

pattern contrasts with that of other nut crops, such as almond and walnut, in which seed and fruit development take place more or less simultaneously during fruit growth (Kester et al. 1996, Pinney et al. 1998). Because of pistachio's unusual pattern of nut development, it incurs the costs of nut fill (kernel growth) over a relatively short period of time (~6 weeks).

There is general agreement that temperate deciduous trees rely on reserve carbohydrates (i.e., stored carbohydrates that accumulate during periods when source supply exceeds sink demand) for early season development because of the absence of a current supply of photosynthates (Kozlowski and Keller 1966, Kramer and Kozlowski 1979, Oliveira and Priestly 1988, Kozlowski 1992). The extent to which reserves are used to support vegetative versus reproductive growth early in the

season depends on their temporal relationship with growth. Most stone fruits and some nut crops rely on reserves for early reproductive development, because anthesis occurs before spring canopy development (Westwood 1993). In other deciduous fruit crops, e.g., apple, anthesis occurs after initial leaf development is nearly complete indicating that reserves are used primarily for vegetative growth and fruit may be dependent on reserves only during their earliest development (Hansen 1971). In pistachio, anthesis is coincident with leaf-out. Thus vegetative growth and early reproductive growth are both likely consumers of reserves. The slightly greater decline in reserve TNC concentration in "on" stems compared with "off" stems from April 9 to June 4 is evidence of demand for reserves caused by fruit development.

Weinbaum et al. (1994) and Rosecrance et al. (1998) hypothesized that the high demand of kernel fill is met by drawing on previous-season reserves, but our data do not support this. Because storage carried forward from the previous season was depleted by the end of Stage I of nut growth (Figures 3 and 4) before the period of rapid kernel fill, the carbon demands of pistachio kernel development during kernel fill could not have been met through use of previous-season storage. We observed in-season mobilization of carbohydrates stored earlier in the same season, corroborating the findings of Nzima et al. (1997a), which explains the unusual nut development pattern of pistachio (Crane and Iwakiri 1981). It appears that pistachio is able to meet high demands of nut fill by storing carbohydrates during Stage II of nut development, when overall demand is low, and then mobilizing this current-season stored carbon during the high demand period of Stage III. Seasonal carbohydrate storage and mobilization data for other temperate deciduous tree crops indicate that no significant in-season mobilization of carbohydrate reserves occurs and, once stored, current-season reserves are not usually mobilized until the following season (Kozlowski and Keller 1966, Oliveira and Priestly 1988). However, an exception to this pattern can occur under stress-inducing or poor growing conditions, as shown for cranberry and primocane-fruiting raspberry (Fernandez and Pritts 1996, Oliveira et al. 2004, 2007, Botelho and Vanden Heuvel 2005).

Based on our data and unpublished values for mean tree growth, we estimated that the amount of TNCs mobilized during kernel fill was about 1.5 kg tree^{-1}. A high pistachio yield is 8.7 kg kernel dry mass tree^{-1} (Weinbaum et al. 1992, Ferguson et al. 2005). Based on the percent of carbohydrates, lipids and proteins in pistachio kernels (USDA 2005) and the approximate glucose cost equivalents for each of these components (Penning de Vries et al. 1983), this yield equates to a total glucose equivalent demand for kernel fill of about 16.7 kg tree^{-1}. Thus, the estimated 1.5 kg of carbohydrates mobilized in season accounted for only about 9% of this demand.

The dramatic decrease in stem TNC concentrations observed at the onset of kernel development provides evidence that carbohydrates may be involved in inflorescence bud abscission (Crane and Nelson 1972, Crane et al. 1973, Wolpert and Ferguson 1990). However, whether the role of carbohydrates in that process is direct, via a starvation mechanism, or

the trigger for a hormonal or other endogenous signal for inflorescence bud abscission remains to be determined. If inflorescence bud abscission could be prevented, would the tree have sufficient carbohydrates available to support a high crop each season? The data presented in Figure 4 indicate that, under well-managed orchard conditions, the stems of trees begin the season with similar TNC concentrations regardless of previous-season crop loads, and stems of "on" and "off" trees end the season with similar TNC reserve accumulation although their TNC concentrations varied significantly during the season.

In conclusion, pistachio appears to have a unique pattern of annual carbohydrate storage and mobilization among temperate deciduous trees, being more similar to some tropical evergreens than to other temperate deciduous trees. Although there were some modest differences in the absolute values of storage reserves in some tissues in trees on the three rootstocks, the general patterns of carbohydrate storage and mobilization were consistent across all rootstocks tested. Mobilization of carbohydrates from current-season, 1-year-old and 2-year-old segments of stems in the same season in which it was stored indicates that pistachio kernel development is supported by in-season mobilization of stored carbon as well as current photosynthesis. Previously, it has been hypothesized that the high demand of kernel fill is met by drawing on the previous-season storage (Weinbaum et al. 1994, Rosecrance et al. 1998), but our data do not support this hypothesis. In-season carbon mobilization may be involved in triggering inflorescence bud abscission and, consequently, alternate bearing. The lack of inflorescence buds in the "off" year may lead to more vegetative growth that could account for the greater total (whole tree) amount of carbohydrate storage following "off" years shown in some studies.

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