

Fruiting and Shading Effects on Metabolic Heat Rates of Inflorescence Buds, Current-year, and One-year-old Shoots of 'Kerman' Pistachio Trees

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ABSTRACT. Isothermal microcalorimetric measurements of metabolic heat rates of 'Kerman' pistachio (*Pistacia vera* L.) individual inflorescence buds, current-year and 1-year-old shoots were used to investigate the roles of current and reserve photosynthates in the abscission of inflorescence buds. In the early stages of development metabolic heat rates of individual inflorescence buds were two and three times those of individual current-year and 1-year-old shoots respectively. Individual shoot organs (1-year-old shoots, current-year shoots, and inflorescence buds) sampled from "on" trees had higher metabolic heat rates than similar individual organs sampled from "off" trees. Artificial shading of pistachio trees for 14 days in early June depressed metabolic heat rates of individual inflorescence buds within 24 h, but there was a delay of 4 days before the decline in metabolic heat rates of individual current-year and 1-year-old shoots. This suggests that metabolic heat rates of individual inflorescence buds apparently depended on currently fixed photosynthates.

Pistachio trees produce heavy crops in alternate years due to the abscission of up to 90% of the inflorescence buds during summer of a heavy cropping ("on") year (Crane, 1984; Crane and Iwakiri, 1987; Crane and Nelson, 1971, 1972; Porlingis, 1974). Bud abscission occurs over two nonoverlapping periods that coincide with active growth of individual vegetative and reproductive structures. About 30% to 40% of the inflorescence buds abscise from "on" and "off" trees between late May and June and bud abscission occurs only on heavily fruiting "on" trees beginning in July and lasting until crop maturity (Crane and Iwakiri, 1987; Porlingis, 1974). Bud abscission in the pistachio has been correlated with available leaf area (Crane et al., 1973; Porlingis, 1974) and with nut load (Crane et al., 1973; Crane and Iwakiri, 1987; Crane and Nelson, 1972; Porlingis, 1974) suggesting competition for resources among different individual "sinks" (Crane, 1971; Crane and Al-Shalan, 1977; Takeda et al., 1980). By the end of the growing season, individual inflorescence buds from "on" trees contain 50% less dry mass and 80% less starch and sugar than do buds from "off" trees (Nzima et al., 1997a, 1997b).

Carbohydrates, nitrogenous compounds and lipids in the form of fats and fatty acids are used in virtually all physiological processes to produce energy, carbon skeletons, and other metabolites for biochemical processes that include the development of new tissues, production of new growth, initiation of reproductive structures, maintenance of vegetative structures, and storage of reserves (Dickson, 1989; Glerum, 1980; Marshall and Waring, 1986; Oliveira and Priestly, 1988; Ryle, 1984; Thornley, 1970).

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Considerable evidence exists that relates respiratory rate of plants to growth rates and productivity and to the rates of plant metabolism (Anderson et al., 1981; Bogie et al., 1976). However, these studies present differing views with positive (Bogie et al., 1976; Geider and Osborne, 1989) and negative (Wilson, 1982; Wilson and Jones, 1982) correlations between respiration rates and plant growth rates.

The evolution of heat from plant tissues under isothermal conditions is a measure of overall metabolic rate (Criddle et al., 1988, 1991; Loike et al., 1981). Unlike respiration, metabolic heat rates also include heat changes associated with all anabolic, catabolic and biochemical processes that do not necessarily involve gaseous exchanges. Thus, measurements of metabolic heat rates of plant tissues provide more integrated measurements of the physiological and biochemical activities of the tissues than measurements of respiration alone (Criddle et al., 1988, 1991).

Artificial shading of pistachio trees for 14 d between 4 and 19 June reduced growth and total nonstructural carbohydrate (TNC) of individual inflorescence buds, current-year and 1-year-old shoots on "off" trees, resulting in bud abscission that was similar to that occurring on "on" trees (Nzima, 1994). Fruiting has been reported to deplete reserves among individual organs of "on" *Citrus paradisi* McFady (citrus) (Goldschmidt and Golomb, 1982; Monselise and Goldschmidt, 1982), *Aesculus californica* Spach (California buckeye tree) (Newell, 1987), and pistachio (Monselise and Goldschmidt, 1982; Nzima et al., 1997a). These results suggest that developing fruits draw their carbohydrates from current photosynthates and reserves stored within individual organs of the tree. If individual inflorescence buds are poor competitors for recently fixed photosynthates as was concluded by Takeda (1980) and Takeda et al., (1980), then metabolic rates of individual buds from "on" trees should be lower than those from "off" trees. Where competition for food occurs basal metabolic rates have been reported to decrease during semi-starvation in a wide range of organisms including humans (Luke and Schoeller, 1992), snails

(Marshall and McQuaid, 1991), fish (Weiser and Medgysey, 1991), rats (Ballor, 1991), and plants (Menegus et al., 1991; Oota et al., 1992). We used isothermal microcalorimetric measurements of metabolic heat rates of individual inflorescence buds, current-year and 1-year-old shoots to investigate the roles of current and reserve photosynthates in the abscission of inflorescence buds among individual 'Kerman' pistachio branches. The results of metabolic heat rates coupled with those on the partitioning of dry mass and on carbohydrate concentrations among individual pistachio branches enabled us to speculate on the mechanism of bud abscission in pistachio trees.

Materials and Methods

The study used a random nine out of 16 experimental 25-year-old 'Kerman' pistachio trees that were described previously (Nzima et al., 1997a, 1997b). Six of the nine trees were in their natural "on" cycle while the other three were in their natural "off" cycle. Artificial shading of the pistachio trees was performed as described previously (Nzima, 1994). Trees were shaded on 4 June and shade was removed on 19 June. Individual leaf photosynthetic rates of the shaded trees were similar to those obtained under cloudy, overcast skies and CO₂ assimilated ranged from 5.00 to 7.33 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

PLANT MATERIALS AND SAMPLING. Six individual branches exposed to the sun (1- and 2-year-old shoots plus or minus nuts and rachises, current-year shoots, leaves and inflorescence buds) were collected from each one of the three unshaded "on" trees, three shaded "on" trees and from three unshaded "off" trees. Only branches with an external diameter <9 mm were collected because the calorimeter sample ampules had internal diameters of ≈ 9 mm. Samples were collected from a height of ≈ 6 m on the western side of each tree between 1300 and 1330 HR and were brought to the laboratory within 45 min. The branches, which were handled carefully to avoid loss of nuts, leaves or buds, were tagged and placed on slightly moist paper towels to maintain humidity and immediately cooled in ice. The ice box was closed leaving an empty space above the plant samples. Samples were collected 1 d before shading, at shading, and 1 d following shading. Thereafter, sampling was done every 2 d until artificial shade was removed on 19 June. Samples were again collected daily for 3 d. After that, samples were collected every 2 d during the subsequent 8 d. Three more samplings were done at 40, 54, and 71 d after shade was first applied.

In the laboratory, individual branches were handled as follows: one or two inflorescence buds were excised from the leaf axils and placed in a sample ampule for measuring metabolic heat. Samples were inspected to ensure the buds were free of insects. A small cross-section of a current-year shoot with an undamaged, intact bark and weighing between 150 and 250 mg (fresh mass) was cut with a razor blade from midway the length of the shoot and placed into a second sample ampule. A similar sized cross section was taken from the midsection of a 1-year-old shoot and placed into the third sample ampule. The three ampules were tightly closed and placed into the chamber of the heat conduction differential scanning calorimeter (DSC) (model 7707; Hart Scientific Inc., Provo, Utah). The order of sample trees was randomized on each sampling date so that no sample from a given tree was measured at the same time of day.

Metabolic heat rates were measured at a constant 25 °C as described by Criddle et al., (1988). Briefly, the Hart Scientific Model 7707 DSC has one reference and three sample ampules each ≈ 1.05 cm³ internal volume. The DSC measures the differences in

the heat flow rate between a metal block and the reference and sample ampules (Criddle et al., 1988). Voltage signal outputs from the calorimeter were interfaced to an IBM-XT computer using an Analog Connection Data Acquisition end control system (Strawberry Tree Inc., Sunnyvale, Calif.). The samples reached a steady state after ≈ 15 min. Each measurement lasted 45 min with heat flow being scanned and recorded every second.

After each measurement, the samples were weighed, dried at 70 °C for 72 h and reweighed. The dry mass was used to convert the measured heat production to heat rates per dry mass of tissue. Heat rates obtained were a measure of metabolic rates of the tissues used (Criddle et al., 1988).

Results

An example of the time course measurements of metabolic heat production at 25 °C using the DSC calorimeter is shown in Fig. 1. The transient changes in heat during the first 15 min represent thermal equilibration between samples and the chambers while the steady state heat rates are the metabolic heat produced by the samples. These data were corrected using baseline curve data for each measurement and ampule and then converted to metabolic heat rates per dry mass of tissue. The mean of heat rates at 18, 24, 30, and 36 min was used as the metabolic heat rate for that individual organ from a specified tree on that particular sampling date. The mean metabolic heat rates of similar shoot organs from three identically treated trees (replications) were analyzed to determine the mean metabolic heat rates for the individual organ.

Generally, individual inflorescence buds had the highest metabolic heat rates averaging two and three times those of individual current-year and 1-year-old shoots, respectively, regardless of whether the trees were unshaded "on" (Fig. 2A) unshaded "off" (Fig. 2B), or shaded "on" (Fig. 2C). The metabolic heat rates of buds, current year and 1-year-old shoots declined with time (Fig. 2 A–C) indicating that as organs matured, their metabolism decreased. Shading resulted in profound changes in metabolic heat production with time (Fig. 2 A and C).

Metabolic heat rates of individual inflorescence buds from unshaded "on" trees increased in early June to above 7 $\mu\text{W}\cdot\text{mg}^{-1}$ dry mass but declined to equal those of individual buds from unshaded "off" trees by 26 to 56 d after 4 June shade (late June through July, Fig. 3). Metabolic heat rates of individual buds from shaded "on" trees were depressed below 6 $\mu\text{W}\cdot\text{mg}^{-1}$ dry mass

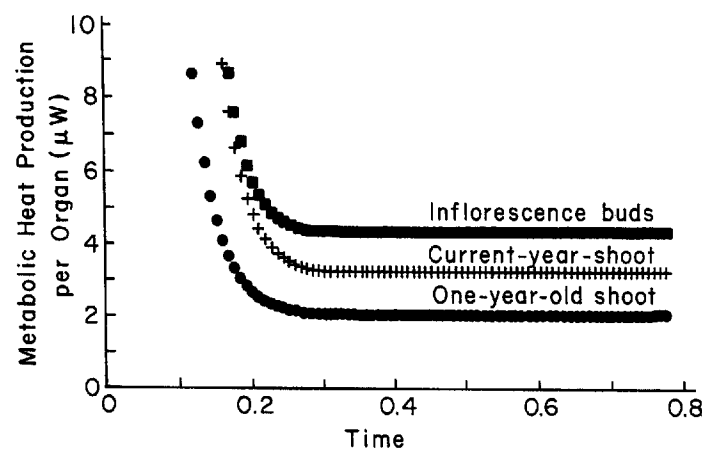


Fig. 1. Time course measurement profiles for metabolic heat produced by inflorescence buds (solid square), current-year shoots (crosses) and 1-year-old shoots (solid circle) of unshaded, 'Kerman' pistachio trees. Data were obtained at 25 °C.

during treatment but were similar to metabolic heat rates of individual buds from unshaded, "on" and "off" trees after shade removal (Fig. 3). There were no samples collected from shaded "on" trees beyond 26 d after 4 June shade since all buds had abscised by then. Metabolic heat rates of individual buds sampled

from unshaded "off" trees were intermediate to those of individual buds from shaded and unshaded, "on" trees until the removal of shade (Fig. 3). Metabolic heat rates of individual buds from unshaded "off" and "on" trees declined gradually with time to $\approx 2.3 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass by 71 d after 4 June shade (mid-August, Fig. 3).

Current-year shoots sampled from unshaded "on" trees had the highest metabolic heat rates in early June and again in July compared with those of current-year shoots sampled from unshaded "off" or shaded "on" trees (Fig. 4). Metabolic heat rates of individual current-year shoots of unshaded "on" trees remained around $4.2 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass for a week after 7 June, before declining significantly to $\approx 2.4 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass after 21 June and further to $\approx 1.4 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass by mid-August (Fig. 4). Shading reduced metabolic heat rates of current-year shoots from $3.5 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass beginning 4 d after shading to $2.3 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass a week later when heat rates remained constant until 26 d after 4 June shade (end of June, Fig. 5). Metabolic rates of current-year shoots sampled from unshaded "off" trees decreased from $3.3 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass 12 d after 4 June shade to $\approx 2.3 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass by 17 d after 4 June shade and further to $1.2 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass 71 d after 4 June shade (mid-August, Fig. 4).

Metabolic heat rates of individual 1-year-old shoots increased in early June before shade (Fig. 5). Furthermore, 1-year-old shoots sampled from unshaded "on" pistachio trees had higher metabolic heat rates compared to those of 1-year-old shoots sampled from shaded "on" and unshaded "off" trees (Fig. 5). Metabolic heat rates of 1-year-old shoots sampled from unshaded "on" trees were fairly constant around $2.6 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass for 2 weeks after 3 d of shade then fluctuated between 2.1 and $2.5 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass from 18 to 21 d after 4 June shade before remaining around $2 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass from 27 to 70 d after 4 June shade (July and August). Shade reduced metabolic heat rates of individual 1-year-old shoots from "on" trees from $2.4 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass to $1.8 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass within 4 d beginning 2 d after shading. Heat rates then increased steadily within 1 d after removal of shade, to $2.3 \mu\text{W}\cdot\text{mg}^{-1}$ dry mass by 11 d later (Fig. 5). The only time that metabolic heat rates of 1-year-old shoots sampled from "on" trees were less than those of 1-year-old shoots sampled from "off" trees was during the shade

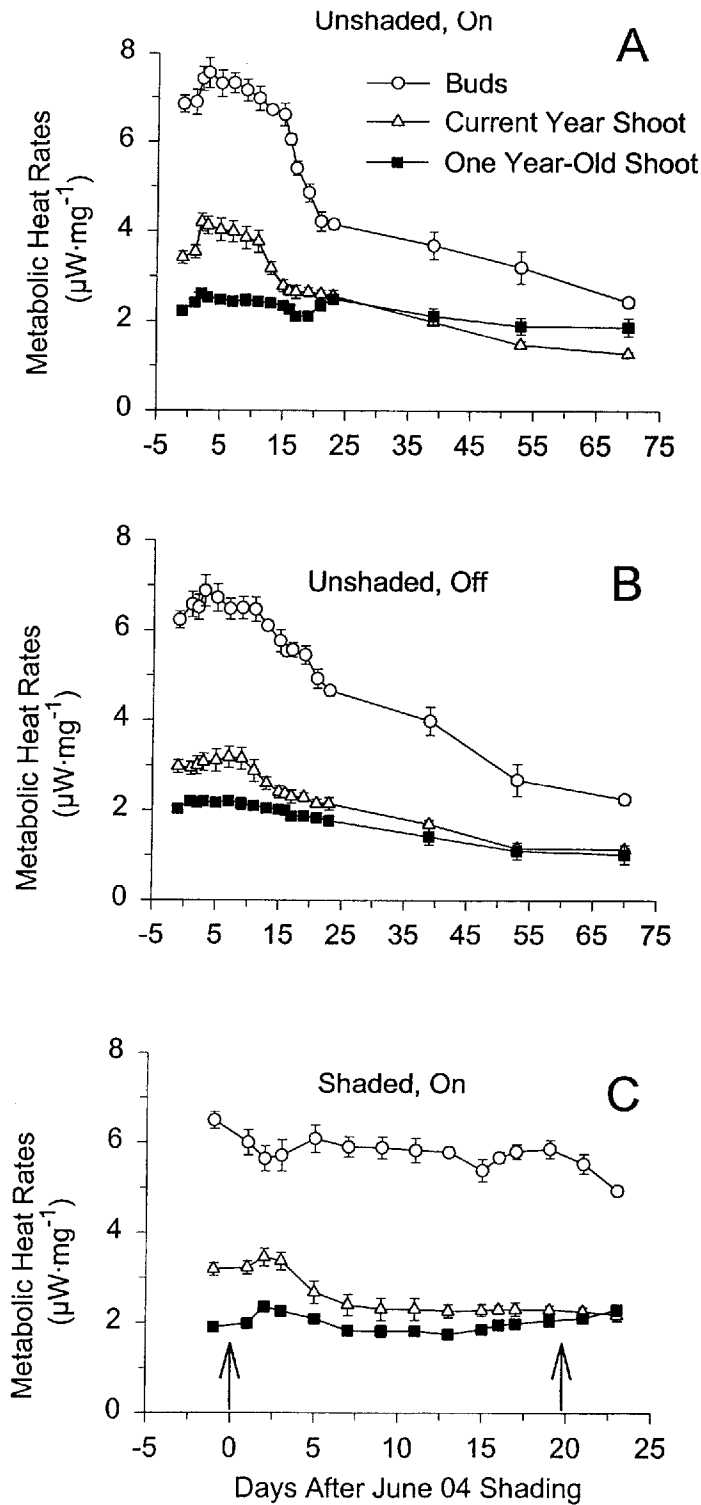


Fig. 2A, B and C. Metabolic heat rates on a dry mass basis of inflorescence buds (open circles), current-year shoots (open triangles), and 1-year-old shoots (solid squares) of unshaded "on" (A), unshaded "off" (B), and shaded "on" (C) 'Kerman' pistachio trees. Trees were shaded 4–19 June. Data were obtained at 25 °C and are means of 12 measurements. Standard error (SE) bars are visible only when larger than symbols.

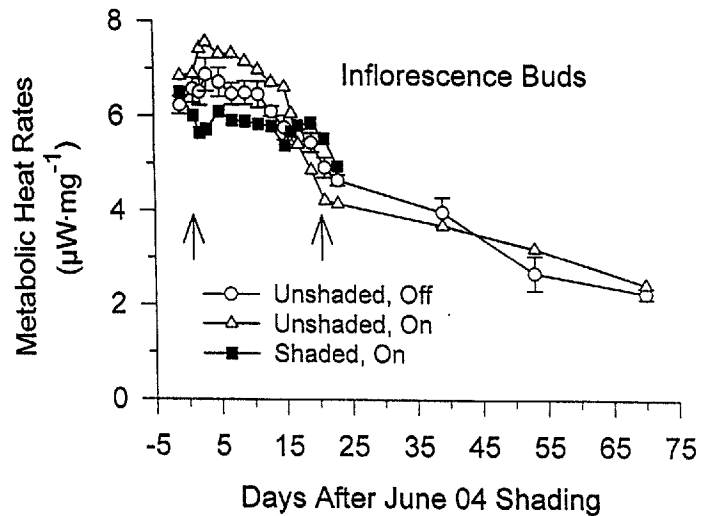


Fig. 3. Time course of metabolic heat rates on a dry mass basis of inflorescence buds sampled from unshaded, "off" (open circles), unshaded "on" (open triangles), and shaded "on" (solid squares) 'Kerman' pistachio trees. Data were obtained at 25 °C and are means \pm SE of 12 measurements. Standard errors are the same for the three treatments. Arrows indicate the artificial shade period 4–19 June. Shaded trees were not sampled beyond 25 d after 4 June because all buds had abscised by then.

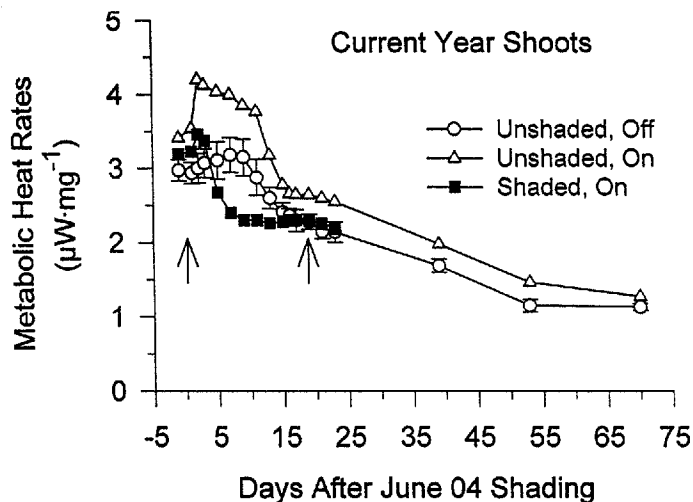


Fig. 4. Metabolic heat rates on a dry mass basis of current-year shoots sampled from unshaded "off" (open circles), unshaded, "on" (open triangles), and shaded "on" (solid squares) 'Kerman' pistachio trees. Data were obtained at 25 °C and are means \pm SE of 12 measurements. Standard errors are the same for the three treatments. Arrows indicate the artificial shade period (4–19 June). Shaded trees were not sampled beyond 25 d after 4 June because all buds had abscised by then.

period. The metabolic heat rates of individual 1-year-old shoots from "off" trees remained fairly constant around 2.2 $\mu\text{W}\cdot\text{mg}^{-1}$ dry mass between 1 and 8 d of shading declined gradually to 1.8 $\mu\text{W}\cdot\text{mg}^{-1}$ dry mass by 26 d after 4 June shade and was 1.0 $\mu\text{W}\cdot\text{mg}^{-1}$ dry mass by 70 d after 4 June shade (Fig. 5).

Discussion

The discussion of these data depart from the tradition of alternate bearing literature in two categories: 1) experimental tree selection with respect to their cropping status and 2) precise terminology within the broad description of alternate bearing.

TREE SELECTION. To reduce experimental variability fruit trees have been historically selected for uniformity in age, size, vegetative growth and cropping status. We agree with tree matching but contend that trees whose flower populations are adjusted by flower removal should not be used for subsequent comparison of chemical constituents with trees whose flower populations are left intact. Trees having similar flower populations are more likely to enter the growing season with comparable quantity of chemical constituents; further, it is likely that in the manipulated, "off" trees ("on" trees deflorated) a feedback mechanism would at least result in early season biosynthetic action contrasting that of the unmanipulated "on" trees that are supplying constituents for the flower-fruit population (Daie, 1985).

A better approach, we contend, is to match experimental trees in their unmanipulated "on" and "off" cycles so that comparison of chemical constituents can be made within the context of the natural alternate cycles.

PRECISE TERMINOLOGY. Alternate bearing describes the result of cropping every other year. This descriptor lacks precision. Species such as *Malus communis* (apple), *Carya illinoensis* Wangeth (pecan), and *Olea europaea* (olive) provided the literature background for early reference to the alternate bearing habit. These species produce few flowers the year of the "on" crop: a problem of flower initiation. In contrast, pistachio initiates a large population of floral buds the year of the "on" crop that later in the year abscise: a problem of floral bud retention. The literature surrounding the former species should emphasize the mechanism(s) of

flower initiation, whereas for pistachio the emphasis should be on the mechanism of retention of initiated floral buds, recognizing that there could be similar features between them.

Individual pistachio inflorescence buds produced the highest metabolic heat rates compared to individual current-year and 1-year-old shoots (Fig. 2) and during this period inflorescence buds were rapidly accumulating dry matter (Nzima et al., 1997a). Arguably, inflorescence buds had the greatest percent of meristematic tissues since they were the latest shoot organs to emerge; moreover, they were still undergoing morphological development (Takeda, 1980; Takeda et al., 1979). The relationships between organ tissue age, composition, and the metabolic heat were highlighted by the data between current-year and 1-year-old shoots whereby the older shoots had the lowest heat rates. The only type of growth that was occurring among 1-year-old shoots was increasing girth. Other experimental evidence suggests that rapidly growing tissues have higher rates of metabolism (Anderson et al., 1981) than nongrowing tissues, although inverse relations have been reported (Hansen et al., 1989; Philbeam and Robson, 1992). In general, our data support the contention that young organs have higher metabolic rates than older ones because of the abundance of meristematic tissues among young organs. However, the differences in heat rates of individual buds and shoots in these experiments cannot be taken to imply that growth rates of individual buds were necessarily greater than those of individual current-year or 1-year-old shoots since we do not know whether these organs have the same respiratory pathways.

The data presented in Figs. 3, 4, and 5 reveal the immediate affect of shade in reducing metabolic heat rates of buds, current-year and 1-year-old shoots and upon shade removal heat rates return to those unshaded comparisons. As well, inflorescence buds, current-year and 1-year-old shoots from unshaded, "on" trees had higher metabolic heat rates than similar organs from "off" trees. These characteristics could be related to the greater concentrations of substrates for metabolism in the buds, current-year and 1-year-old shoots of "on" trees following a noncropping year compared with similar organs of "off" trees (Nzima et al., 1997b).

The immediate depression of metabolic heat rates of individual buds by shading of trees suggest that the primary substrates for

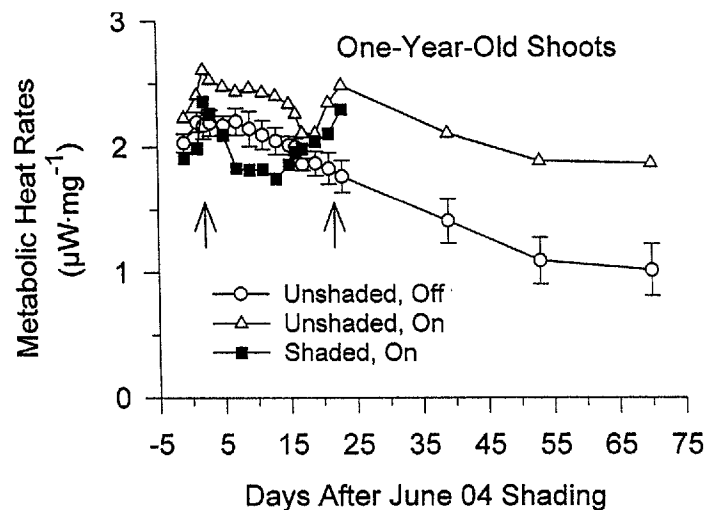


Fig. 5. Time course of metabolic heat rates on a dry mass basis of 1-year-old shoots sampled from unshaded "off" (open circles), unshaded, "on" (open triangles), and shaded "on" (solid squares) 'Kerman' pistachio trees. Data were obtained at 25 °C and are means \pm SE of 12 measurements. Standard errors are the same for the three treatments. Arrows indicated period of artificial shade (4–19 June). Trees that had been shaded were not sampled beyond 25 d after 4 June.

metabolism in the buds were recently fixed photosynthates. On the other hand, the heat rates of individual current-year and 1-year-old shoots increased until the fourth day after shading implying that metabolism in these organs may have depended on current photoassimilates and on stored reserves. However, it is possible that the high metabolic rates in these shoots were transient, reflecting active transport between source and sink or remobilization of resources within the organs. The metabolic heat rates of individual buds on shaded, "on" trees began to increase after 4 d of shading (Fig. 3) indicating that the buds had either adapted to shade stress or that substrates for metabolism had become available. The latter seems probable especially since the increase in bud metabolic heat rates coincided with the decrease in the metabolic heat rates of individual current-year and 1-year-old shoots (Figs. 4 and 5). Reduction in metabolism within these shoots would have meant a decrease in demand for carbohydrates metabolic substrates. Furthermore, it seems reasonable to assume that the metabolism of developing nuts was also decreased by shading, therefore reducing competition for resources (carbohydrates) between inflorescence buds and nuts. These comparisons are akin to what has been observed in humans, fish, snails and plants. For example, the basal metabolic rates (BMR) of lean individuals were greatly reduced by under feeding while those of obese individuals were only moderately reduced, but the mass of obese individuals declined as fat was used to maintain the moderate BMRs (Luke and Schoeller, 1992). Sagisaka et al. (1991) reported a tendency by winter wheat to maintain metabolic substrates under snow cover through a reduction in metabolic activities.

Metabolic heat rates of individual buds from unshaded, "on" trees declined gradually between 8 June and 21 June, a period corresponding with lignification of the endocarp (Crane et al., 1973; Crane and Iwakiri, 1981; Porlingis, 1974) and with the first wave of bud abscission (Crane, 1986; Crane and Iwakiri, 1987). Since the decline in metabolic heat rates coincides with the decline of TNC that was reported previously (Nzima et al., 1997b), we conclude that low carbohydrate concentrations among individual buds may be directly correlated to the abscission of inflorescence buds.

In our earlier paper (Nzima et al., 1997a) we presented evidence that individual current-year shoots produced on "on" trees were generally smaller in diameter compared to those produced on "off" trees. This could result in low metabolic heat rates among current-year shoots from "off" trees, as reported in our current paper, because of a larger proportion of wood tissue on these thicker shoots. However, only branches with an external diameter less than 9 mm were sampled from "off" and "on" trees thus the differences in shoot diameters were minimized. Moreover, "on" trees would have had slightly larger 1-year-old shoots since these were produced the previous "off" year. Despite these observations, 1-year-old shoots sampled from unshaded "on" trees still had higher metabolic heat rates (Fig. 5), a trend that was true for all the sampled organs.

Conclusions

Alternate bearing in pistachio occurs in a fashion unique among fruit trees in that differentiated inflorescence buds form and abscise the year of the "on" crop (Crane and Nelson, 1971). On the basis of our research over two alternate bearing production cycles in naturally "on" and "off" pistachio trees we conclude that the abscission of inflorescence buds in the "on" year results from the following: that although "on" trees enter the growing season with greater carbohydrate reserve than "off" trees, demands of cropping

substantially reduce inflorescence bud mass by seasons end (Nzima et al., 1997a) a time when more carbohydrate accumulates in "off" than "on" tree organs, particularly inflorescence buds (Nzima et al., 1997b). The effect of shading for 14 d in June decreases photosynthesis, accelerates inflorescence bud abscission and loss of dry mass in other organs (Nzima, 1994). Finally, photosynthetic rate is lower among "on" than "off" tree leaves (Nzima, 1994) and combined with the high metabolic heat rates in "on" tree inflorescence buds, current-year, and 1-year-old shoots, directly results in loss of dry mass and subsequent inflorescence bud abscission (this paper).

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