Alternate Bearing in Pistachio as a Masting Phenomenon: Construction Cost of Reproduction versus Vegetative Growth and Storage

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ABSTRACT. Whole-tree effects of alternate bearing on the reproductive growth, vegetative growth, and carbohydrate storage in mature pistachio (scion *Pistacia vera* L., rootstock *Pistacia atlantica* Desf.) were examined. Although it is generally accepted that the “off” year in pistachio may be used to accumulate carbohydrate reserves, it was found that starch and sugars from the “off” year equaled only 8% of the construction cost of the “on” year’s fruit load. The dry mass increase in perennial woody tissue of roots, trunk and branches in the “off” year (20.2 kg/tree), was 75% of the mass of fruit in “on” trees (26.4 kg/tree). When construction cost of wood and fruit is considered, “off” year woody tissue growth is 64% of “on” year fruit growth. Since previous studies have shown that leaf dry mass is generally 30% greater in “off” than “on” pistachio trees, we conclude that the overall production of biomass in “off” and “on” year pistachio is similar. Therefore, we suggest that the “off” year is not a period of substantial storage carbohydrate accumulation, but rather a switch in allocation from reproductive to vegetative growth. This is consistent with ecologically based theories of the adaptive advantage of masting behavior, and suggests that withholding water and fertilizer during the “off” year may not harm “on” year yield.

Alternate, biennial, or irregular bearing occurs in many fruit trees and is especially pronounced in pistachio. In pistachio, inflorescence buds are formed 1 year before bloom, but abscise during years of a large crop (the “on” year), causing a small crop the following year (the “off” year). Many horticultural reviews have been written about alternate bearing in general (Davis, 1957; Jonkers, 1979; Singh, 1948; Sparks, 1974) and pistachio specifically (Crane and Iwakiri, 1981; Monselise and Goldschmidt, 1982). In the two most recent reviews, two hypotheses for alternate bearing in pistachio are proposed. The carbohydrate competition hypothesis states carbohydrate competition between fruit and buds causes bud abscission. In contrast to this, the hormone hypothesis states hormones from the fruit or leaves cause bud abscission. Both explanations maintain that limited resources are the evolutionary cause of alternate bearing and either of the two hypothesized physiological mechanisms (physiological causes) are suspected to prevent overcropping and tree death (Goldschmidt and Golomb, 1982).

Alternate bearing has also been studied from an ecological perspective, but is usually called masting. Alternate bearing, biennial or irregular bearing, and masting are all considered to be different types of the same phenomena. Alternate and biennial bearing are synonyms for a nonbearing interval of 2 years (regular bearing has a 1-year interval). The term irregular bearing describes a variable nonbearing interval of ≤ 2 years. Masting describes all nonbearing intervals from 1.5 to 140 years. See Harper and White (1974), Janzen (1971) and Janzen (1976) for reviews of masting.

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The mast year happens when there is a synchronous production of a large seed crop. Masting is seen as a “defensive strategy which satiates seed predators in mast years and starves them in intervening periods...” (Silvertown, 1980). By masting, the tree can increase the number of seeds that survive compared to a constant seed output strategy (Waller, 1979). A key element in these explanations from the ecological literature is that masting is a switch between vegetative and reproductive partitioning for reasons other than a resource limitation.

In deciduous trees, like pistachio, there may a resource limitation of carbohydrate during early spring, since then there are no leaves and all growth depends on storage. In pistachio, increased carbohydrate storage has been observed after an “off” year (Crane et al., 1976; Crane and Al-Shalan, 1977; Nzima et al., 1997; Weinbaum et al., 1994). This additional storage may increase the photosynthetic capacity of the “on” year tree by enabling quick canopy expansion. This additional photosynthetic capacity may make it possible for an “on” year pistachio to produce large quantities of fruit. But to our knowledge this idea has not been quantitatively tested in pistachio. Many authors suggest that the additional carbohydrate storage is used directly for fruit growth, as tested in Goldschmidt and Golomb (1982) in citrus. They found, in a 15-year-old alternate bearing ‘Wiking’ mandarin, that “off” year carbohydrate storage accounted for 50% of “on” year yield by comparing dry masses of storage and yield. Weinbaum et al. (1994), used a chemical balance equation approach to determine the number of carbon atoms in the fruit and indirectly suggested that “off” year storage of carbohydrate supplied carbon needed for “on” year fruit growth in pistachio.

We propose to also compare “off” year storage to “on” year yield, by reanalyzing carbohydrate storage (starch) and dry mass data previously published by Weinbaum et al. (1994), using a construction cost approach. Construction cost is the amount of energy required to produce a net gain in dry mass (Chiariello et al., 1989). The construction cost approach includes the number of carbon atoms lost during growth respiration, while the chemical

balance equation and dry mass comparison methods do not include this carbon.

In pistachio, vegetative growth of wood and leaves may also be a large carbon sink and may reduce the amount of carbon available for storage. We propose to estimate the yearly growth of wood (above and below ground) on mature pistachio trees, using the yearly increase in trunk cross-sectional area (TCSA) and converting TCSA to dry mass of wood. We can convert TCSA to dry mass by using a relationship based on the whole-tree dry mass measurements on excavated trees of Rosecrance et al. (1996) and trunk cross-sectional measurements made by us on those same trees. By measuring the change in TCSA on neighboring trees a few meters away, we can track whole-tree wood growth over many "on" and "off" year cycles.

Little fruit growth occurs in pistachio during "off" years and carbohydrate energy usually put into fruit can be used for storage or wood dry mass increase. The purpose of this study is to a) determine the amount of energy invested in "off" year carbohydrate storage in pistachio and b) determine the amount of energy invested in "off" year wood production. The relative importance of wood growth and storage during the "off" year will be determined by comparing these two "off" year measurements to "on" year yield. Since wood, storage carbohydrate, and fruit require different amounts of energy, per gram, to gain dry mass, we will use a construction cost approach to control for this difference.

Materials and Methods

CONSTRUCTION COST CALCULATIONS. Construction cost of wood, storage carbohydrate, and fruit can be determined by proximate analysis (Chiariello et al., 1989; Penning de Vries et al., 1974.) Briefly, the amount of glucose needed for carbon skeletons, reducing equivalents and ATP for the construction of carbohydrates, protein, fats and other compounds present in large amounts (such as lignin) is calculated. By determining the quantity of these compounds in the plant tissues, one can then multiply the cost of producing these compounds in grams of glucose per gram of compound by the grams of the compound present. The result is construction cost in grams of glucose equivalents ($\text{g}\cdot\text{g}^{-1}$).

Values for the construction cost of many biological compounds are available in the literature, as are the approximate concentrations of these compounds in pistachio tissues (or other similar plants). The concentrations of biological compounds in the pistachio kernel was taken from Ferguson and Kader (1995) in a report on the nutritional value of the kernel for human consumption. The concentrations in the hull were taken from Labavitch et al. (1982) in a study to determine the suitability of hulls for consumption by cattle. Within the nut, final percent dry mass of kernel, hull and shell were determined to be 44%, 12%, and 44%, respectively from Crane and Al-Shalan (1974), who measured 200 to 300 fruit weekly on 11-year-old trees in Winters, Calif. The construction cost of oak leaves (Mooney and Hays, 1973) was used as an approximation for the construction cost of pistachio leaves.

No literature values were found for pistachio shells and wood. Therefore shell (collected from bins of hulled pistachio during the 1996 harvest in Winters, Calif.) and wood samples (from 1995–96 winter prunings with a minimum diameter of 5 cm in Kettleman City, Calif.) were ground and analyzed by a commercial lab (J&L Analytical Services, Inc., Modesto, Calif.). Concentration of crude fat (ether extract method), crude fiber (fritted glass crucible method), crude protein (combustion method, then $\text{N} \times 6.25$), lignin (acid insoluble lignin method), and ash (2 h at 600 °C) were used. References for each method of determination are found in the

Association of Official Analytical Chemists (AOAC) Official Methods of Analysis (OMA) 920.39, AOAC OMA 978.10, AOAC OMA 942.05, AOAC OMA 973.18, and ash by combustion, respectively (Helrich, 1990).

CARBOHYDRATE STORAGE. Mature pistachio trees were excavated with a back hoe, weighed whole, and starch concentration was determined, as part of a previously published study in mineral nutrition by Weinbaum and colleagues (Brown et al., 1995; Picchioni et al., 1997; Weinbaum et al., 1994). We have converted the starch, wood, fruit and leaf dry mass data from this previous experiment to glucose equivalents, using the construction cost values as described above. Briefly, the Weinbaum and colleagues experiment was conducted in a 1969 planting of 'Kerman' pistachio trees on *Pistacia atlantica* Desf. rootstock, in an experimental orchard in Winters, Calif. All flowers on three of six adjacent 15-year-old trees were removed in April, 1984 (an "on" year). This created "on" and "off" trees in the same season. Complete alternation of cropping was maintained by stripping flowers from "off" trees during the spring of each year (1984 to 1991). Trees were fertilized annually between 1988 and 1990 with $(\text{NH}_4)_2\text{SO}_4$ at the rate of 1.5 kg N/tree and excavated during the dormant season on 15 Jan. 1991. Whole-tree fresh mass was recorded and chipped samples were weighed fresh, reweighed after drying, and a total tree dry mass was determined. Samples were saved for later nutrient analysis. Starch concentration was measured by hydrolysis of ethanol insoluble material and then standard enzymatic methods as outlined by Sturgeon (1990). Soluble sugar concentration was not determined in the trees from these studies (Brown et al., 1995; Picchioni et al., 1997; Weinbaum et al., 1994), but these values were available from the same cohort of trees from the same orchard, from the 1991 and 1992 growing seasons (Nzima, 1993). Nzima (1993) reported very small differences in concentration of soluble sugars at the end of the growing season for "on" and "off" scaffold branch wood, but they are included in our analysis because soluble sugars can be a significant form of storage carbohydrate in some trees (Oliveira and Priestley, 1988). The soluble sugar concentration data for scaffold branches was used for our construction cost analysis as an estimate of whole-tree soluble sugar concentration. Nzima (1993) did not measure the concentration of soluble sugars in roots.

Whole-tree dry mass values for wood, nuts, leaves, starch (Weinbaum et al., 1994) and soluble sugars (Weinbaum et al., 1994; Nzima, 1993) were converted to glucose equivalents (this study), to determine the energy required to construct those parts (or compound). We then compared the glucose equivalents present in starch and soluble sugars to the glucose equivalents present in fruit on a whole-tree basis. The statistics presented for this data are those performed by Weinbaum et al., (1994) on their dry mass data (one-way ANOVA, Statview 2, Abacus Concepts, Berkeley, Calif.). No additional statistics were performed on our converted construction cost values because dry mass data was taken from published mean values.

ESTIMATED GROWTH OF WOOD AND ACCUMULATED ANNUAL BIOMASS. Two groups of trees (16 and 12 trees) were used to estimate wood growth and accumulated biomass. These trees are the same trees as described in Rosecrance et al. (1996), as part of a study in mineral nutrition.

The first group of 16 trees were excavated whole as part of the Rosecrance et al. (1996) study. We used the whole-tree dry mass data from Rosecrance et al. (1996) and additional trunk cross-sectional measurements made by us, to determine the relationship of above and below ground perennial dry mass to TCSA. In the second group of 12 trees, yearly changes in growth ring width

Table 1. Summary of the cropping status (visually verified) for three groups of 'Kerman' pistachio trees grown in Madera, Calif. Naturally synchronized trees were in their natural bearing state. Naturally unsynchronized trees were also in their natural bearing state, but out of synchrony with the majority of the trees in the block. Stripped trees had all fruit removed in May 1992 to force the trees into an alternate bearing pattern out of synchrony with the majority of trees in the block. Average fruit mass values with different letters are significantly different at $P = 0.05$ level according to a Duncan test (Proc GLM, SAS Inst., Cary, N.C.)

		Year					
Tree		1991	1992	1993	1994	1995 ^c	1996
group		Tree cropping status					
A	Naturally synchronized (n = 6)	Off	On	Off	On	Off (6.3 ± 11.3 a)	On
B	Naturally unsynchronized (n = 3)	On	Off	On	Off	On (24.3 ± 5.5 b)	Off
C	Stripped unsynchronized (n = 3)	Off	Off	On	Off	On (28.4 ± 0.94 b)	Off

^aDry fruit (kg/tree).

(1990 to 1997) and fruit yield (1995 only) were measured by us. This second group of 12 trees was also used by the Rosecrance et al. (1996) study, but for mineral nutrition measurements unrelated to our current study. The Rosecrance et al. (1996) data was used only to verify cropping status of these trees as "on" or "off" from 1992 to 1994 (Table 1). Whole-tree wood growth in the second group of 12 trees was then estimated from changes in annual growth ring width, converted to trunk cross-section, then to wood mass, using the trunk cross-section to wood mass relationship generated in the first group of 16 trees. Both groups of trees grew side by side in a 1972 planting of 'Kerman' pistachio trees on *Pistacia atlantica* Desf. rootstock in a commercial orchard in Madera, Calif. Row by tree spacing was 9.1×4.6 m.

As reported in Rosecrance et al. (1996) the excavations of the first group of 16 trees were conducted on three dates in 1994 (24 May, six trees, 8 Sept., four trees, and 31 Dec., six trees). Fresh mass of all tree parts, including leaves when present, was recorded. Samples were chipped, weighed fresh, reweighed after drying, and total tree dry mass was determined. Samples were saved for later nutrient analysis. Starch concentration was not measured. Trunk circumference was measured by Rosecrance et al. (1996) once in February 1994, and wedge shaped pieces of trunk, 3 to 4 cm thick and comprising about one-quarter of the TCSA, were saved from each subsequent excavation. These trunk wedges were used by us to determine the increase in TCSA from the time of the February 1994 circumference measurement, until excavation. Since only a portion of the trunk cross-section was available, we estimated the TCSA at the time of excavation by taking the average of three radial measurements from the 1994 growth ring to the cambium. We then added this additional growth to the February 1994 measurement and modeled the trunk cross-section as a circle. A regression comparing TCSA, at the time of excavation, to the mass of all woody tissue in the tree at this time (sum of roots, trunk, branches, and new woody shoots) was made (Proc REG, SAS Inst., Cary, N.C.).

The regression of TCSA to woody tissue mass was used to calculate the yearly growth of wood in the second group of 12 additional trees. Trees were visually classified as "on" (heavily cropping) or "off" (<2 kg fruit/tree), by Rosecrance et al. (1996), during 1992, 1993, and 1994. Trees were divided into three groups based on their pattern of alternate bearing (Table 1). Group A trees (n = 6) were unmanipulated and their cropping pattern was naturally synchronized with the majority of trees in the block. Group B trees (n = 3) were also unmanipulated and were naturally unsynchronized with most trees in the block. Group C trees (n = 3) were naturally synchronized with the majority of trees in the block in 1991, but had their flowers stripped during May, 1992, causing them to become unsynchronized with most trees in the block. Yield (kg fruit/tree) was measured on 3 Oct. 1995, for all trees (Table 1)

as part of a root respiration study (Stevenson, 1998). The mass of fruit left in the tree after shaker harvesting were visually estimated by a person experienced in hand harvesting and weighing such fruit. The value was almost 0 for "off" trees and <1 kg dry mass for "on" trees. This visual estimate was added to the measured yield.

On 4 Apr. 1997, cores were taken from groups A, B, and C trees using a 16-mm coring, high speed drill bit attached to an electric drill to a depth of ≈ 40 mm. Three horizontal cores from each tree, facing S, NE, and NW were taken at the point of smallest trunk diameter above the graft union and below the primary scaffolds. The trunk circumference at the position of the cores was taken at this time. Cores were then sliced in half with a band saw and the resulting flat face was brushed vigorously with a stiff wire brush to accentuate the annual growth rings. Size of annual growth rings was measured from the time of coring to the beginning of 1991. The change in TCSA, calculated from the size of the growth rings, was converted to wood growth for each year, using the regression from the 16 trees excavated in 1994. Excavated trees were at least two trees spacings (30 ft) away from cored trees and both groups of trees grew within a 10 row by 23 tree area.

A first approximation of annual accumulated biomass per tree was calculated. The wood growth and fruit yield, in 1995, for the 12 cored trees was added to the 1994 leaf mass. The total mass (kg/tree) and construction cost (kg/tree) of wood, fruit, and leaves grown during "on" and "off" years was compared. No statistics were used in this comparison since leaf mass values came from a different year than wood and fruit, although the trees were of similar age and size.

Results

CONSTRUCTION COST. The construction cost for 6 classes of compounds and the mass percentage of each of the compounds found in different pistachio tissues (Table 2) were used to calculate the construction cost for each pistachio tissue type (first column of Table 3). Pistachio fruit are the most expensive tissue because of the large amount of lipids in the kernel (Table 2).

CARBOHYDRATE STORAGE. The 1991 whole-tree dry mass data (Weinbaum et al., 1994) was converted to glucose equivalent (GLU eq.) (Table 3). The total amount of energy in storage carbohydrate after an "off" year (9.82 kg GLU eq. starch + 7.88 kg GLU eq. soluble sugars = 17.7 kg GLU eq. nonstructural carbohydrates/tree) represents $\approx 22\%$ of the "on" year crop (81.5 kg GLU eq. fruit/tree). When the difference in stored carbohydrate between "off" and "on" years (17.7 kg GLU eq. - 11.27 kg GLU eq. = 6.43 kg GLU eq. nonstructural carbohydrates/tree) is compared to the difference in yield (81.5 kg GLU eq. - 3.6 kg GLU eq. = 77.9 kg GLU eq. fruit/tree), carbohydrate storage after an "off" year accounts for only 8% of the energy needed to construct the "on" year's crop.

Table 2. Construction cost (mass glucose to produce unit mass of compound, $\text{g}\cdot\text{g}^{-1}$) and chemical composition of pistachio. The top half of the table gives construction cost in glucose equivalents for six major chemical constituents of plant tissues. The bottom half of the table gives the mass fraction (%) of these chemicals in four tissues of pistachio. The reference column contains the literature source for that row of data. Helrich (1990) does not contain source data but is the reference for the laboratory methods used in making the chemical percentage determinations.

	Lipids	Protein	Carbohydrates	Phenols	Lignin	Ash	Reference
Construction cost ($\text{g}\cdot\text{g}^{-1}$)	3.03	1.62	1.2	1.9	2.58	0	Chiarello et al. (1991)
Tissue	Mass (%)						
Kernel	56.3	20.6	28.9	---	---	3.2	Ferguson and Kader (1995)
Hull	4.4	4.7	80	6.9	5 (est.)	---	Labavitch et al. (1982)
Shell	0.52	0.62	85.9 ^y	---	12.9	0.1	Helrich (1990)
Wood	1.8	3.5	73.9 ^z	---	19.0	1.8	Helrich (1990)

^{y,z} Values in table are higher than measured and are the difference between the sum of noncarbohydrate components and 100%. Actual values are 49.9% and 69.6%, respectively.

Table 3. Whole pistachio tree mass data from trees grown in Winters, Calif. (Weinbaum et al., 1994) converted to energy cost in glucose equivalents ($\text{g}\cdot\text{g}^{-1}$) per tree. Soluble sugar estimate (est.) made from concentration data in Nzima (1993) multiplied by root, trunk, and branch mass of Weinbaum et al. (1994). Masses of starch and sugar were subtracted from roots, trunk, and branch mass to avoid counting those compounds twice.

Tissue type or storage compound	Construction cost ($\text{g}\cdot\text{g}^{-1}$)	Dry mass (kg/tree)		GLU eq. (kg/tree)	
		On	Off	On	Off
New shoots	1.5	3.4 ^{***}	4.9	5.1	7.35
Leaves	1.6	16.0 ^{ns}	23.0	25.6	37.8
Fruit	1.8	45	2	81.5	3.6
Roots, trunk, branches	1.5	345.6 ^{ns}	331.2	518.4	496.8
Starch	1.2	3.35 ^{***}	8.18	4.02	9.82
Soluble sugar	1.2	6.04 (est)	6.57 (est)	7.25	7.88
Sum	---	419.4	375.9	641.87	563.25
Sum (excluding ns values)	---	73.8	44.7	123.47	66.45

^{ns, **, ***} Nonsignificant or significant at $P \leq 0.05$ or 0.01 , respectively, according to F test as reported in Weinbaum et al. (1994).

ESTIMATED GROWTH OF WOOD AND ACCUMULATED ANNUAL BIOMASS. Regression analysis suggests a close relationship between TCSA in cm^2 and dry mass of trunk, roots, and branches in kg (MASS) (Fig. 1). Hence, the yearly change in TCSA should give a reasonable estimate of the yearly mass increase of woody perennial tissue, which is consistent with the results of Pilsbury and Kirkley (1984). The regression equation for this relationship is $\text{MASS} = 0.693 \times (\text{TCSA}) - 104.3$ ($R^2 = 0.88$, $F = 98.7$, $p < 0.0001$, $n = 16$). The mean total woody dry mass was not significantly different between "off" (252 kg/tree) and "on" (225 kg/tree) trees ($F = 2.86$, $p = 0.11$, $df = 15$, Proc GLM, SAS Inst., Cary, N.C.).

Growth rings in pistachios generally show clear alternate bearing patterns with thick rings during "off" years and thin rings during "on" years. For naturally synchronized trees (group A, Fig. 2) the yearly estimated wood growth from 1991 to 1996 was high during "off" years and low during "on" years. Naturally unsynchronized trees (group B) did not show such a large difference in wood dry mass increase between "on" and "off" years, but did show the same inverse relation of wood growth to fruit yield as exhibited in group A. Before the 1992 stripping treatment, stripped trees (group C) had the same wood growth as group A. From 1993 onward, group C trees exhibited the same annual pattern of increases and decreases as exhibited by group B, consistent with the newly established pattern of fruit yield in group C. The year-to-year differences in wood growth in group C were much smaller than either group A or B, until 1995–96, when the difference in wood growth was similar to that of group B.

During 1995, "off" year dry mass increase of perennial woody tissue in the roots, trunk, and branches (20.2 kg/tree, Fig. 2), was 75% of the mass of fruit in "on" trees (26.4 kg/tree, Table 1). When

construction cost of wood and fruit is considered, "off" year wood growth is 64% of "on" year fruit growth.

Wood and fruit growth (1995), and 1994 leaf growth (Rosecrance et al., 1996) of "on" and "off" year annual accumulated biomass were compared (Fig. 3). During the "on" year, 18% more biomass was accumulated than during the "off" year. On a construction cost basis, 24% more GLU eq. were accumulated annually by "on" trees.

Discussion

The reanalysis of whole-tree data from Weinbaum et al. (1994), using a construction cost approach, shows the amount of carbohydrate stored after an "off" year amounts to only 8% of the energy need for an "on" year crop. On this basis, carbohydrate storage in alternate bearing pistachio does not provide a substantial amount of energy or biomass for the overall construction of the "on" year crop. Carbohydrate storage is probably important for early spring growth (Kozłowski, 1992), but the relative importance of carbohydrate storage for early spring growth between "on" and "off" years is not known.

Annual accumulated biomass or its construction cost may be somewhat greater in "on" than in "off" years (Fig. 3), but the maintenance respiration of the additional mass of roots in "off" trees (Rosecrance et al., 1996) could account for the difference in accumulated biomass (Kozłowski, 1992). In addition, blank nuts (hollow fruit) were not considered separately in the construction cost calculations used in our analysis. Since blank nuts contain no kernel, their construction cost will be lower than that of filled nuts, and the construction cost for the entire fruit load of the tree will be less as the percentage of blank nuts increases. This could also account for some of the difference in annual accumulated biomass.

Fig. 1. Regression of trunk cross-sectional area (TCSA) versus total dry mass of woody perennial tissue (MASS) in the pistachio trees from Madera, Calif. This regression ($\text{MASS} = 0.693 \times (\text{TCSA}) - 104.3$, $R^2 = 0.88$, $F = 98.7$, $p < 0.0001$) was used to calculate the growth of perennial wood, by measuring trunk growth.

In any case, the difference in whole-tree biomass between "on" and "off" trees is only 9.2 kg while the difference in fruit is 24.7 kg. Therefore, the main consequence of alternate bearing is not a substantial increase in biomass production during the "on" year, but rather a change in partitioning between vegetative (wood) and reproductive (fruit) growth.

Pistachio trees stripped of fruit in an "on" year will produce fruit out of synchrony with neighboring trees and this treatment has been used as an experimental control to provide "on" and "off" trees during the same year. If alternate bearing involves a coordinated pattern of growth, vegetative growth one year and reproductive growth the next, and stripping treatments only change the reproductive component, then the behavior of stripped trees may not be entirely analogous to that of normally alternating trees. It is interesting to note that the pattern of wood growth in stripped trees is not altered as predictably as fruit production, particularly in the first few years following stripping (Fig. 2). It may be prudent to restrict consideration of alternate bearing in pistachio to comparisons between trees that have been unsynchronized for a number of years, as suggested by Nzima et al. (1997).

If carbohydrate limitation is not an overriding consideration as a physiological or evolutionary cause for alternate bearing in pistachio, it may be appropriate to consider other evolutionary reasons for alternate bearing or masting. Evolutionary reasons for masting include satiating seed predators (Janzen, 1976), optimizing vegetative and reproductive growth in a random weather environment (Lalonde and Roitberg, 1992), reducing competition between sibling trees (Ravishanker et al., 1995; Uma Shaanker et al., 1988), keeping canopy fruit load above a certain threshold to attract dispersers (Murray, 1987; Stapanian, 1982), and maximizing pollination success (Janzen, 1976). The ecological literature also includes resource limitation as a factor contributing to masting (Harper and White, 1974) but resource limitation is only one hypothesis of many, and is not considered to be the dominant factor, as in the reviews of Crane and Iwakiri (1981), Davis (1957), Jonkers (1979), Lakso (1994), Monselise and Goldschmidt (1982), Singh (1948), Sparks (1974), and Wardlaw (1990).

Patterns of carbohydrate partitioning in woody perennials are different than in annuals (Begon et al., 1996). Annual plants always maximize seed production in a single growing season. A resource limitation is often a good explanation for reduced yield of fruit in annual plants. However, perennial plants display allocation patterns that sometimes postpone reproduction during certain years in favor of storage or vegetative growth (Iwasa and Cohen, 1989; Lalonde and Roitberg, 1992). In the case of perennial plants, a reduced yield of fruit is sometimes not caused by a resource limitation, but by a change in allocation patterns. Perennials have optimized allocation patterns that maximize reproductive output over their lifetime, which can be very long. Pistachios, for example, almost never flower until their fourth year and sometimes not until their eleventh year (D. Parfitt, personal communication) and can give good yields after 700 years of age (Whitehouse, 1957). The selection pressure on a wild grown tree in a pre-agricultural population of pistachio may have favored long life with variable yields over a shorter life with large annual yields. The alternate bearing habit in pistachio may be better explained as a means to maximize lifetime cumulative fitness, following ecological theory, rather than a mechanism for maximizing a particular year's "on" crop.

A more comprehensive study measuring wood dry mass increase, leaf dry mass, fruit yield, and carbohydrate storage for whole "on" and "off" trees over many years would be desirable. Unfortunately, that was not possible in this study due to cost and complexity. Fortunately, we were able to supplement existing studies (Rosecrance et al., 1996; Weinbaum et al., 1994) with additional information, and obtain estimates of overall construction cost of "on" and "off" pistachio trees. We believe that our analysis of these data provides valuable information, because it suggests that "off" year carbohydrate storage is small and that "off" year wood growth is very large. The wood dry mass increase data (Fig. 2) spans multiple years and shows that wood growth in pistachio can be over 5900 kg·ha⁻¹. We suggest further whole-tree studies in alternate bearing pistachio to determine if such large

Fig. 2. Annual growth of wood, from 1991 to 1996, in all parts of the tree from the 12 cored pistachio trees growing in Madera, Calif. Group A synchronized trees expressed "on" and "off" year fruiting patterns in synchrony with most trees in the block. Group B, unsynchronized trees, were naturally unsynchronized with most trees in the block. Group C, unsynchronized by stripping in 1991, were originally group A trees, until 1991, when they were stripped of fruit to force them into synchrony with group B trees. Error bars are ± 1 standard error.

Fig. 3. Estimated total accumulated biomass for "on" and "off" trees growing in Madera, Calif. Wood and fruit biomass are from the 12 cored trees during 1995. Biomass of leaves is from four neighboring trees (2 "on", 2 "off") as measured in 1994 by Rosecrance et al. (1996). Total mass = the sum of wood, fruit, and leaves. GLU eq. = the construction cost of wood, nuts, and leaves in glucose equivalents ($\text{g}\cdot\text{g}^{-1}$).

amounts of "off" year wood growth are necessary for the following "on" year's yield. Another topic for further study is the analytical methods for determination of structural carbohydrates in pistachio shells. The crude fiber method (AOAC OMA 978.10 in Helrich, 1990) used for shells was developed for cattle feed, and although apparently suitable for ground pistachio wood, it is apparently not suitable for use on pistachio shells, since measured and calculated values did not closely agree (Table 2).

If alternate bearing in pistachio is an ecologically adaptive trait, rather than a physiological requirement for "off" year carbohydrate storage, then this may have a number of practical implications. One is that selecting a variety with continued high production each year should be physiologically possible. Another implication is the potential usefulness of reducing cultural inputs during the "off" year as a management strategy for the strongly alternate bearing 'Kerman' variety. Water and fertilizer applied to "off" trees may mainly serve to increase vegetative growth of pistachio, and promote associated weed and insect pest pressure. The cost of pruning vegetative growth in pistachio is significant (Ferguson et al., 1995). Minimal water and fertilizer applications during the "off" year (off year minimal management or OYMM) could reduce vegetative growth and pruning costs without reducing "on" year yield. If OYMM also caused greater synchrony in pistachio trees (Kanber et al., 1993) then it may be useful to maintain selected blocks of trees out of synchrony with other blocks and allow more efficient use of harvest equipment. OYMM could have other economic and environmental benefits as well, such as decreasing the risk of developing pesticide resistant pest populations (Raffa, 1989). It may be valuable to initiate a long term study of OYMM, not only as a potentially more sustainable agricultural practice, but also to further test the importance of "off" year carbohydrate storage and wood growth to "on" year yield.

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