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Leaf Development, Dry Matter Accumulation, and Distribution within Branches of Alternate-bearing 'Kerman' Pistachio Trees

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Abstract. We investigated the development of leaf area (LA) and the distribution of dry matter within branches of 25-year-old, alternate-bearing 'Kerman' pistachio (*Pistacia vera* L.) trees that were in their natural "on" (heavy) or "off" (light) bearing cycles to determine the immediate and delayed effects of fruiting on shoot growth. Compared to "off" trees, individual leaves of "on" trees were greater in number and expanded twice as fast during the first 30 days after full bloom (FB) (FB + 30). Mature, fully expanded leaves of "on" trees were smaller (124.1 ±3.26 cm^2) than those from "off" tree (163.3 ±3.40 cm^2), indicating delayed demands of fruiting on initial leaf growth. Total LA per current shoot was greater in "on" than "off" trees because shoots of "on" trees averaged eight leaves, compared with six for "off" trees. More inflorescence buds per shoot (seven vs. three buds) abscised from "on" than from "off" trees. About 60% of the young developing nuts had abscised by FB + 30 when they weighed <250 mg each and another 25% abscised between FB + 30 and FB + 60 when individual nuts weighed ≈400 mg. The average total dry mass (DM) of individual branches of "on" trees increased 1322% (5·9 to 83·9 g) compared to 598% (4·2 to 29·3 g) in "off" trees. Besides nuts, leaves accumulated the greatest amount of dry matter within individual branches followed in decreasing order by current wood, 1-year-old wood, and inflorescence buds. DMs of individual leaves of "on" trees averaged between 15% and 48% greater than leaves of "off" trees. "Off" trees invested 4.6 g of dry matter into individual 1-year-old wood and 2.1 g into current wood. "On" trees, however, invested 1.3 g of dry matter into 1-year-old wood and 4.3 g of dry matter into current wood. One-year-old wood was an important major source of carbohydrates for developing leaves, current wood, rachises, and nuts. The immediate demands of fruiting on individual components of a branch were measured as losses in DMs. Individual leaves, current wood, 1-year wood, and rachises lost 1.1%, 0.3%, 1.1%, and 1.0%, respectively, of the average total DMs of individual branches of "on" trees. This loss was equivalent to 5.7%, 5.9%, 26.7%, and 16.4%, respectively, of the seasonal average peak DMs of the respective individual components of the branch.

In contrast to other alternate-bearing species, heavy ("on") and light ("off") pistachio crops result from the summer abscission of ≤90% of preformed inflorescence buds on heavily producing trees (Crane and Iwakiri, 1987; Crane and Nelson, 1971; Monselise and Goldschmidt, 1982; Porlingis, 1974; Wolpert, 1985). This condition is undesirable because it affects management factors such as cash flow, labor needs, and use of farm machinery. The actual mechanism(s) involved in pistachio bud abscission remains unclear. Another enigma of the pistachio tree is that extension growth of new shoots is depressed during the light crop year instead of during the heavy crop year.

Most pistachio inflorescence buds abscise during the period of rapid seed development (Crane and Nelson, 1972; Crane et al., 1973), suggesting competition between inflorescence buds and developing nuts for carbohydrates and other resources (Crane and Al-Shalan, 1977; Porlingis, 1974; Takeda et al., 1980) or influences of growth regulators produced in developing seeds that are transported to buds (Crane et al., 1976; Pontikis, 1990). Inflorescence bud abscission itself has been correlated with available leaf area (Crane et al., 1973; Porlingis, 1974), available carbohydrates (Crane et al., 1976; Porlingis, 1974; Takeda et al., 1980), and seed development and the number of nuts (Crane and Iwakiri, 1987; Crane and Nelson, 1972; Crane et al., 1973; Porlingis, 1974; Wolpert, 1985; Wolpert and Ferguson, 1990), thus suggesting competition for resources. To our knowledge, the currently available data are insufficient to conclusively show how seed growth promotes bud abscission or how the correlations between carbohydrate concentrations and bud abscission are causally related.

Data in the literature suggest that the critical periods for inflorescence bud abscission are those associated with vegetative budbreak and growth of new shoots (late March to May), rapid increase in pericarp mass (April to May), lignification of the endocarp (mid May to June), and rapid increase in seed mass (July to August) (Crane, 1986; Crane and Iwakiri, 1981; Monselise and Goldschmidt, 1982; Porlingis, 1974; Takeda et al., 1979). However, the major problems with previous investigations on pistachio by Crane and Al-Shalan (1977), Crane et al. (1973 and 1976), Porlingis (1974), Takeda et al. (1980), and Wolpert and Ferguson (1990), as well as similar investigations on other fruit trees (Post and Stam, 1983; Roper et al., 1988; Stutte and Martin, 1986), are that these studies were performed on deflorated or defruited trees that were otherwise in their natural heavy crop cycles. Trees with manipulated crops may not represent the true physiological status of trees with unmanipulated crops during their light crop years.

Trees in their natural "on" bearing cycle enter the growing

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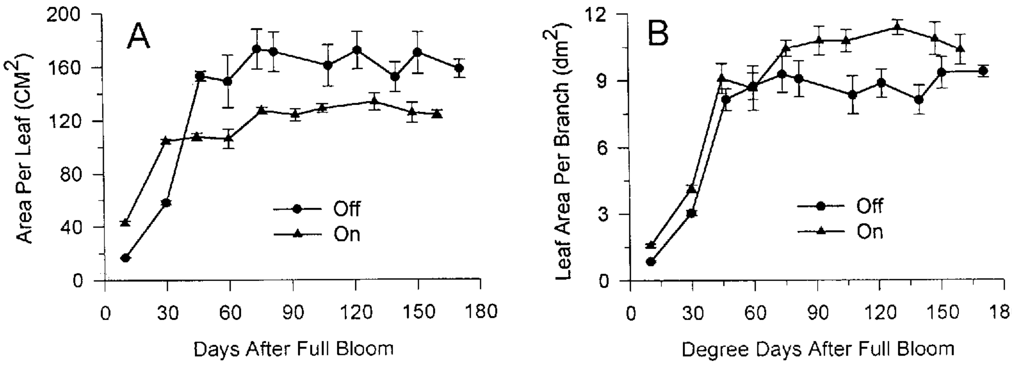

Fig. 1. Development of leaf area of individual leaves (**A**) and of total leaf area of individual branches (**B**) during a complete alternate bearing ("on" + "off") cycle of 'Kerman' pistachio trees. Each data point is a mean and SE of the mean differences for six sampled branches each from four "on" and four "off" trees. Trees that were "on" in 1991 were "off" in 1992 and vice versa. Respective data are averaged over the 2 years.

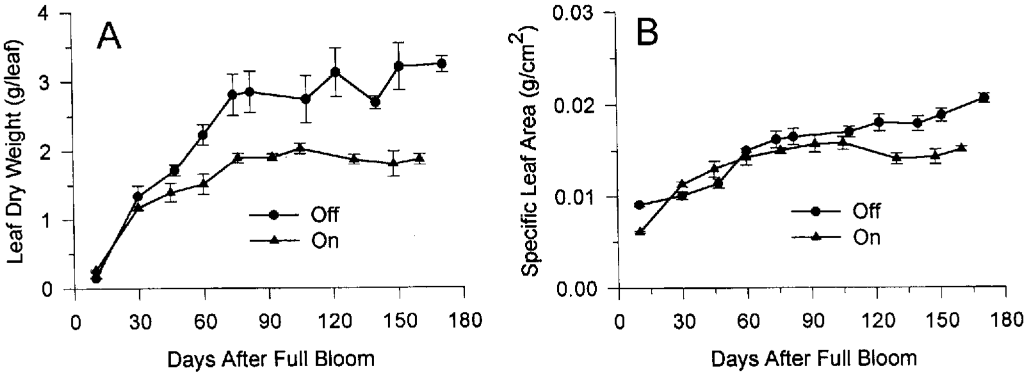

Fig. 2. Variations in leaf dry mass (**A**) and specific leaf areas (**B**) of "on" and "off" 'Kerman' pistachio trees. Data points represent means and SEs of the mean differences for leaves of six branches each from four "on" and four "off" trees in 1991 and 1992.

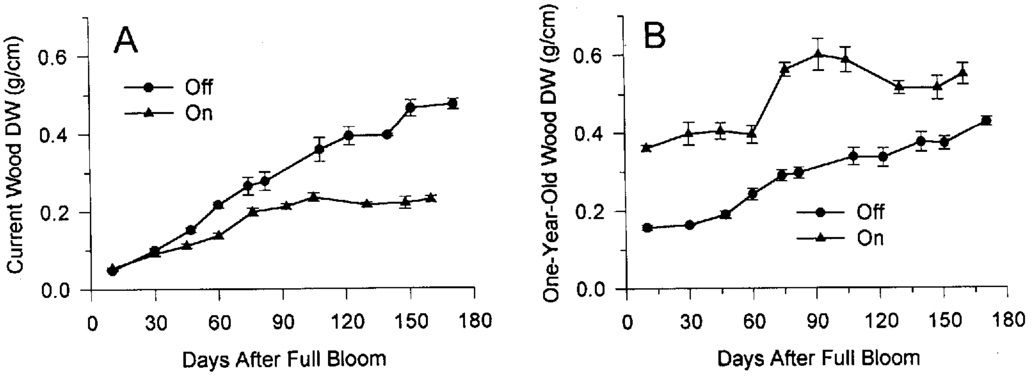

Fig. 3. Average dry mass per centimeter length accumulated in individual current wood (**A**) and in 1-year-old wood (**B**) of "on" and "off" 'Kerman' pistachio trees. Data points represent means and SEs of the mean differences for six branches each from four "on" and four "off" trees during 1991 and 1992, averaged, respectively, over the complete alternate-bearing cycle.

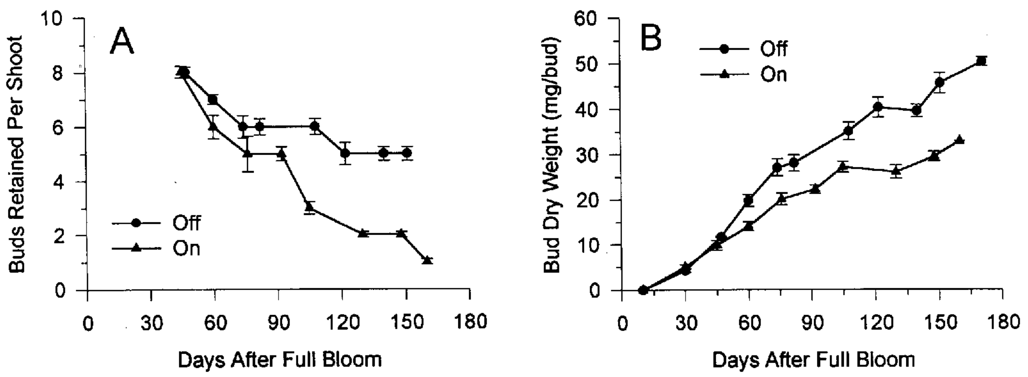

Fig. 4. Bud retention (**A**) and dry masses of individual buds (**B**) on current wood of "on" and "off" 'Kerman' pistachio trees. Data are means and SE of mean differences for thirty current shoots each from four "on" and four "off" trees (**A**) and six branches each from four "on" and four "off" trees in 1991 and 1992.

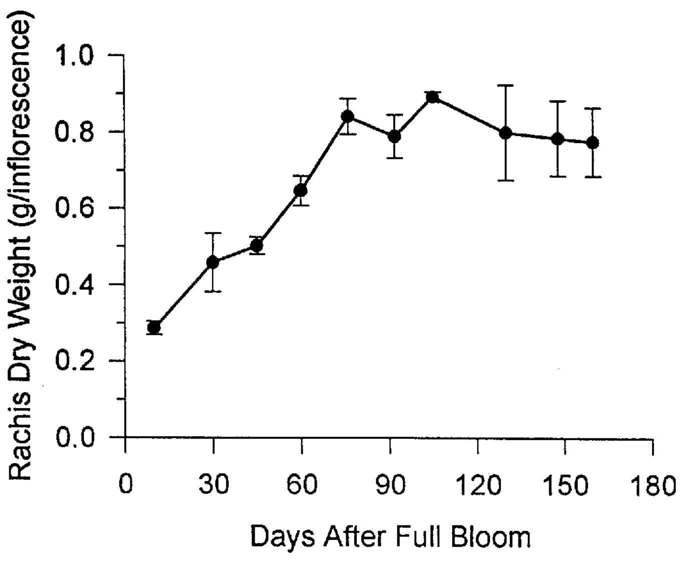

Fig. 5. Average dry masses of individual rachises of "on" 'Kerman' pistachio trees. Data are means and SEs of the mean differences for rachises of six branches each from four "on" trees in 1991 and 1992.

season with a large carbohydrate reserve following the "off" year, which would make it impossible to identify the role of carbohydrates in bud abscission during the "on" year. This position stems from the common view that stored reserves play a significant part in initial fruit growth and that developing fruit impose an immediate, as well as a delayed, limit to vegetative growth. Thus, we preferred to use pistachio trees with unmanipulated crops that were in their natural alternate-bearing cycles. In our paper, data will describe when dry matter accumulates within an individual pistachio tree branch (1-year-old wood plus current shoot) and dry matter potential contribution to the developmental physiology of shoots on alternate-bearing 'Kerman' trees to demonstrate the effects of fruiting on the growth of vegetative organs and inflorescence buds.

Materials and Methods

EXPERIMENTAL TREES. Eight 25-year-old *Pistacia vera* 'Kerman' trees on *Pistacia atlantica* Desf. rootstock were selected for uniform size, crop load, leafiness, and leaf color at the Wolfskill Expt. Orchard, Winters, Calif., during Summer 1990. Trees were spaced 6.1 m between and along the rows. Four of the eight trees were in their natural "on" cycle, whereas the other four were in their "off" cycles in 1991 and in their respective alternate "off" and "on" cycles in 1992. Each tree had three primary scaffold branches arising from the main scion trunk. Standard commercial practices for weed control, fertilization, and irrigation of the trees were followed during the experiment.

PLANT MATERIALS AND SAMPLING DATES. Pistachio trees bear nuts on 1-year-old wood, whereas leaves and inflorescence buds are produced on current-year shoots. Thus, the crown of a pistachio tree consists of a collection of leafless branches (metamers) terminating in leafy growths (current-year shoots) at the periphery of the crown. The new shoots consist of pinnately compound leaves, each subtending a single inflorescence bud in their axils and a vegetative bud at the terminus. Because of strong apical dominance, lateral vegetative buds on previous year's wood generally do not grow unless the terminal buds in current shoots are removed. The method used to collect sample branches removed the apical dominance and resulted in more vegetative shoots emerging during the following year than would have been the case without sampling. A sample branch consisted of 1-year-old wood, the current shoot (wood + leaves + inflorescence buds), and rachises and nuts. Samples were collected beginning 10 d after full bloom (FB) (FB + 10) and about every 14 to 21 d thereafter in 1991 and 1992.

Six branches were collected at random from each of the four "off" and four "on" trees, with 11 sample dates in 1991 and 10 sample dates in 1992. The initial cut was made on 2-year-old wood. In the field, the branch was dissected into 1-year-old wood, rachises, nuts, leaves, current wood, and inflorescence buds. These samples were kept in a large ice box and brought into the laboratory where they were stored at –30 °C.

INFLORESCENCE BUD ABSCISSION. We tagged 30 current shoots per tree at random around the lower, middle, and upper parts of each tree's canopy. With "off" trees, we included only shoots that had a crop during the previous "on" cycle. All inflorescence buds on these individual branches were counted on 20 and 29 May, 5 and 19 June, 3 July, 6 and 27 Aug., and 25 Sept. to monitor bud abscission during Spring and Summer 1991 and 1992.

LEAF AREA (LA) AND DRY MASS OF LEAVES, INFLORESCENCE BUDS, SHOOTS, RACHISES, AND NUTS. The total number of leaves, inflorescence buds, and nuts on the six sampled individual branches of four "on" and four "off" trees were counted for each sample date in the field. Samples were removed from –30 °C storage and freeze-dried in a drier (model 20 SRC-X; Virtis Co., New York).

Individual branch total LA and dry mass were determined after freeze-drying. Sixteen leaf disks were punched out from leaf samples that represented all leaves within each individual branch using number seven cork borer that was ≈1.43 cm^2. Total LA per branch was estimated as the product of the leaf disks' area and the quotient of total leaf dry mass per shoot and leaf disk dry mass.

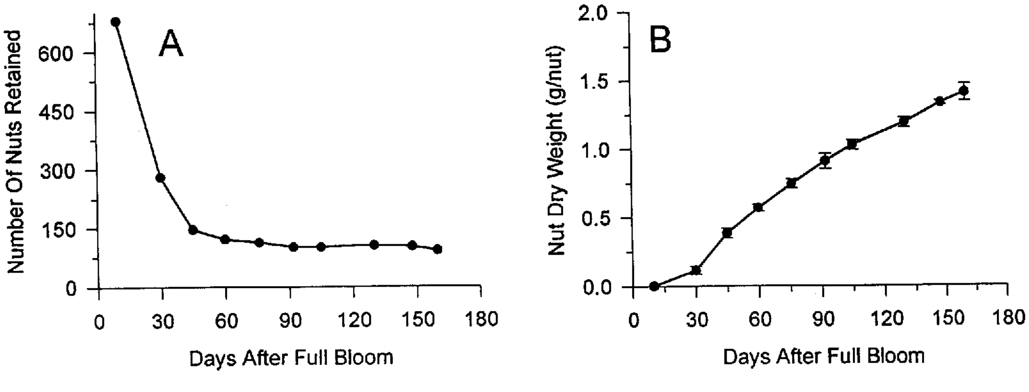

Fig. 6. Number of nuts on individual bearing branches (A) and dry masses accumulated by individual nuts (B) of 'Kerman' pistachio trees. Data are means and SEs of the mean differences for nut counts from six branches of four trees and 420 nuts for dry masses.

Table 1. Effects of heavy ("on") and light ("off") cropping on total dry masses (DM) (in grams) of various components of individual branches of 'Kerman' pistachio trees. Data are DM means and their SEs for a complete bearing cycle in which the "on" and "off" trees in 1991 were respectively "off" and "on"in 1992.

Branch	Sampling dates [days after full bloom (FB)][z]									
	FB + 10		FB + 30		FB + 47/45		FB + 60		FB + 74/76	
component	Off	On	Off	On	Off	On	Off	On	Off	On
	1	2	3	4	5	6	7	8	9	10
Leaves	1.0 ± 0	1.9 ± 0.1	8.0 ± 0.6	9.4 ± 0.6	9.3 ± 0.8	9.9 ± 1	13.1 ± 0.7	11.9 ± 1	15.1 ± 1.2	15.6 ± 1
Current wood	0.1 ± 0	0.4 ± 0	0.3 ± 0	1.2 ± 0.2	1.5 ± 0.1	1.8 ± 0.2	0.9 ± 0.1	2 ± 0.2	1. ± 0.1	3.5 ± 0.4
1-year-old wood	3.1 ± 0.2	1.3 ± 0.1	3.1 ± 0.1	1.4 ± 0.2	3.0 ± 0.2	2.1 ± 0.5	3.3 ± 0.3	1.7 ± 0.2	5. ± 0.2	2.6 ± 0.3
Inflorescence buds	---	---	0.02 ± 0	0.04 ± 0	0.06 ± 0	0.07 ± 0	0.12 ± 0	0.08 ± 0	0.14 ± 0	0.09 ± 0
Rachis	---	1.3 ± 0.1	---	2.5 ± 0.2	---	2.8 ± 0.2	---	3.5 ± 0.3	---	5 ± 0.2
Nuts	---	1.0 ± 0.1	---	8.6 ± 0.5	---	15.8 ± 0.8	---	24.1 ± 1.5	---	33.7 ± 1.6
Whole branch[y]	4.2 ± 0.9	5.9 ± 0.2	11.4 ± 1.9	23.1 ± 1.7	12.9 ± 2.1	32.5 ± 2.5	17.4 ± 3	43.3 ± 3.8	21.2 ± 3.4	60.5 ± 5.2

[z] Where sampling date did not coincide in 1991 and 1992, the days after FB are given as FB + 47/45. The first number refers to FB + 47 for 1991 and the second to FB + 45 for 1992.

[y] Calculated as the sum of DMs of leaves, current wood, 1-year-old wood, rachis, nuts, and inflorescence buds in 1991 and 1992 averaged over the 2 years for "on" and "off" trees, respectively.

$$\text{LA per branch} = \frac{\text{Total leaf dry mass per shoot}}{\text{Total leaf disc dry mass}} \times \text{Total leaf discs area}$$

Average dry mass of inflorescence buds was determined from the DMs of all buds in the six individual branches taken per tree from four "on" and four "off" trees (total of 24 samples).

The total lengths and DMs of individual 1-year-old and current wood of all sampled branches per tree were measured, and the amount of dry matter accumulated per centimeter of length was calculated from the corresponding total DMs and lengths.

Rachises and nuts were separated after drying, and their total DMs were determined. The mean individual nut DM per branch was determined from a random sample of 105 whole nuts (including pericarp) after all deformed nuts were discarded.

DATA ANALYSIS. The data collected during 1991 and 1992 were measurements of various aspects of plant growth across time. A repeated-measures analysis of variance (ANOVA) and MANOVA were performed on the DMs using the general linear models procedure of SAS (SAS Inst., Cary, N.C.).

Results

The data on leaf area and DMs of the individual organs were compared based on days after FB and degree days after FB to determine whether differences in leaf area and DMs during the 2 years were due to temperature effects. The results from these comparisons were generally similar; therefore, all data are presented in relation to days after FB only.

EFFECT OF ALTERNATE-BEARING ON LEAF NUMBER PER BRANCH, AREA PER LEAF, TOTAL LA PER BRANCH, AND LEAF DM PER BRANCH. "On" trees averaged eight leaves (range seven to 10) per shoot compared with six leaves (range five to seven) for "off" trees. The number of leaflets per leaf was variable and inconsistent, ranging from one to five on "off" and "on" trees. Individual leaves of "on" trees grew faster than those of "off" trees during the first 30 d after FB, but mature, fully expanded leaves of "on" trees were 24% smaller (124.1 ± 3.26 cm^2) than those of "off" trees (163.3 ± 3.40 cm^2) (Fig 1A). In contrast, "on" trees had greater total LA per individual branch (Fig. 1B) because of differences in leaf number per branch. DMs per leaf were similar for "on" and "off" trees before FB + 45; thereafter, individual leaf DMs for "off" tree leaves were substantially greater throughout the season, averaging between 15% and 48% more than leaf DMs for "on" tree leaves (Fig. 2A). Specific leaf area increased steadily among leaves of "on" and "off" trees but declined among leaves of "on" trees after FB + 105 (Fig. 2B).

EFFECT OF ALTERNATE BEARING ON CURRENT- AND 1-YEAR-OLD-WOOD LENGTHS AND DMS. Current wood produced by "on" trees was longer than current wood produced by "off" trees. Similarly, 1-year-old wood of trees in their "off" cycle was longer than that of trees in their "on" cycle because the wood was produced during the previous "on" and "off" cycles, respectively. Average DM per centimeter length of individual current wood of "on" and "off" trees increased by 400% and 1000%, respectively, during the growing season (spring and summer) and was also greater for "off" than for "on" trees (Fig. 3A). Average DMs of individual current wood of "on" trees were similar from FB + 105 until harvest (Fig. 3A).

Generally, average DM per centimeter length of individual 1-year-old wood of "on" trees grew to twice its size at the beginning of the growing season for "off" trees, length increased to three times its beginning size. "On" and "off" trees showed different growth patterns (Fig. 3B). DM per centimeter length of individual 1-year-old wood of "on" trees were constant between FB + 10 and FB + 60 and then rapidly between FB + 60 and FB + 92 before declining thereafter (Fig. 3B). In contrast, DM per centimeter length of individual 1-year-old wood of "off" trees increased gradually and consistently throughout the season and remained less than the comparative DMs of 1-year-old wood of "on" trees.

EFFECT OF ALTERNATE BEARING ON INFLORESCENCE BUD ABSCISSION AND DMS. The initial numbers of inflorescence buds on current wood of "on" and "off" trees in late May were similar (Fig. 4A). However, more inflorescence buds abscised from individual wood of "on" than "off" trees (seven vs. three buds, respectively), especially after FB + 92 (from July onward). Average DMs of inflorescence buds from "on" and "off" trees were similar during the first 45 d after bloom, but thereafter, individual buds from "on" trees accumulated less dry matter than did those from "off" trees (Fig. 4B).

RACHIS DM AND NUMBERS AND DM OF NONABSCISING NUTS. On average, there were six inflorescences on individual 1-year-old wood (range: five to seven). Rachis DM per inflorescence increased rapidly between FB + 10 and FB + 76 before remaining constant (Fig. 5). About 60% of nuts on individual bearing shoots abscised (from 700 to 300 nuts per shoot) between FB + 10 and FB

Table 1. Continued.

Sampling dates [days after full bloom (FB)]^z									
FB + 82/92		FB + 108/105		FB + 122/130		FB + 140/148		FB + 171/160	
Off	On	Off	On	Off	On	Off	On	Off	On
11	12	13	14	15	16	17	18	19	20
14.7 ± 1	16.6 ± 0.7	16.2 ± 1.1	16.9 ± 0.8	16.1 ± 1.3	15.9 ± 0.6	17.3 ± 0.7	15.5 ± 1.1	19.2 ± 0.6	15.6 ± 0.9
1 ± 0.1	4.2 ± 0.4	1.2 ± 0.1	4.3 ± 0.3	1.4 ± 0.2	4.6 ± 0.3	1.5 ± 0.1	4.6 ± 0.5	2.1 ± 0.2	4.3 ± .0.3
5.9 ± 0.4	3.5 ± 0.5	6.2 ± 0.4	2.9 ± 0.4	7.1 ± 0.4	2.3 ± 0.2	7.6 ± 0.5	2.6 ± 0.4	8.2 ± 0.5	2.6 ± .0.2
0.15 ± 0	0.09 ± 0	0.19 ± 0	0.05 ± 0	0.21 ± 0	0.03 ± 0	0.23 ± 0	0.02 ± 0	0.27 ± 0	0.03 ± 0
---	5.3 ± 0.4	---	5.3 ± 0.4	---	4.3 ± 0.2	---	4.7 ± 0.3	---	4.4 ± 0.2
---	38.8 ± 2.7	---	43.3 ± 3.5	---	52 ± 2.9	---	56.9 ± 4.6	---	57 ± 3.8
21.8 ± 3.3	65.8 ± 5.9	22.8 ± 3.2	72.8 ± 6.7	24.8 ± 3.6	79.1 ± 8.9	26.6 ± 3.2	84.3 ± 8.8	29.8 ± 4.3	83.9 ± 8.9

+ 30 when individual nuts weighed ≈250 mg; another 25% abscised between FB + 30 and FB + 60 (Figs. 6A). Individual bearing shoots had 100 to 160 nuts at harvest. Average DMs of individual nuts increased slowly during the first 30 d after FB before increasing linearly until harvest (Fig. 6B).

EFFECT OF ALTERNATE BEARING ON THE AMOUNTS AND DISTRIBUTION OF DRY MATTER. Average total DMs for individual branches of "on" trees increased by 1322% from 5.9 to 83.9 g/branch between FB + 10 and FB + 160 (April to September) compared to a 598% increase in total DM of individual branches of "off" trees (4.2 to 29.3 g/branch) (Table 1). Average total DM for individual current wood of "on" and "off" trees increased 10- and 27-fold from 0.4 to 4.3 vs. 0.1 to 2.1 g/branch, respectively, during the same period. In contrast, total DMs for individual 1-year-old wood only doubled from 1.3 to 2.6 vs. 3.1 to 8.2 g, respectively, for "on" and "off" trees (Table 1). Leaves, 1-year-old wood, current wood, and inflorescence buds contained 69%, 26%, 5%, and 1%, respectively, of the total DM of individual branches of "off" trees (Table 1). In comparison, nuts consisted of 63% to 70%, leaves 20% to 25%, current-year wood 5%, 1-year-old wood 4%, and inflorescence buds 0.1% of the total DMs of individual branches of "on" trees. When total DMs of nuts were excluded from the total DMs of individual branches of "on" trees, leaves accounted for 72%, current wood 16%, 1-year-old wood 12%, and inflorescence buds 0.3% of the total DM of bearing vegetative branches.

Discussion

Plant growth and productivity are largely determined by the amount of carbon fixed and how this is distributed among vegetative, reproductive, and storage organs (Chalmers and Van Den Ende, 1975; Gifford and Evans, 1981; Watson, 1984), signifying a great dependence on the development, performance, and behavior of the source–sink systems. In our study, we found individual leaves of "on" 'Kerman' pistachio trees were 2 to 3-fold more in number and expanded twice as fast during the first 30 d after bloom but matured and senesced earlier than those of "off" trees. These results suggest that individual branches of "on" trees had sufficient resources at leaf emergence to prime leaf area expansion. Subsequent competition from other organs may have resulted in early leaf maturation and senescence, however. The initial rapid development of "on" tree–leaf area also implied that these leaves became sources much earlier, thus contributing to the supply of resources to other developing organs (sinks). New deciduous leaves have a positive feedback on the production process (Schulze et al., 1983), while the role of evergreen leaves includes rapid photosynthetic recovery during the early part of the growing season to accumulate additional resources for growth of new organs (Kimura, 1969).

The slow growth of the smaller, earliest emerging leaves on individual branches of "off" trees may indicate the delayed costs of the previous year's heavy cropping. Newell (1987) found that branches of *Aesculus californica* Spach (California buckeye tree) that had fruited the previous year produced leaves that were smaller and light yellow in color the following year. Similarly, the reduction in leaf size on individual branches of "on" pistachio trees is comparable to those reported for *Prunus avium* L. ('Lambert' sweet cherry) (Kappel, 1991), *Olea europaea* (olive) (Rallo and Suarez, 1989), *Malus communis* (apple) (Avery, 1970; Maggs, 1963), and the California buckeye tree (Newell, 1987). The major difference between the cited examples and pistachio is that total leaf area per branch was greater in "on" than in "off" pistachio trees. The opposite is true for sweet cherry, olive, apple, and the California buckeye tree. Typically, 'Kerman' pistachio trees behave similarly to the biennial monocarp, *Atrium tomentosum* Mill., whose total leaf area during the "on" years is 5-times greater and develops within 7 weeks compared to 20 weeks during "off" years (Heilmeier et al., 1986). We can speculate on two distinct roles for the earliest emerging leaves in pistachio trees: 1) a contribution to the subsequent growth of bigger leaves on individual branches of "off" trees, and 2) for "on" trees, a provision of a large leaf area per branch (Fig. 1B) for carbon assimilation and export to 1-year-old wood, developing nuts, and storage.

The data on specific leaf area suggest that leaves from individual branches of "on" trees were thinner than those of "off" trees perhaps because of less chlorophyll and protein content, fewer or smaller cells, or less structural and nonstructural materials (Forney and Breen, 1985; Marini and Barden, 1981; Roper and Kennedy, 1986; Thomas, 1990; Wooge and Barden, 1987). Individual leaves of "on" trees had less dry matter between FB + 30 and FB + 92 (Fig. 2A), probably because resources were remobilized from them during the period of rapid development of seeds (FB + 92 to FB + 148) indicated by the decline in specific leaf area. Data in Table 1 show an average loss of 0.94 g in total DM of leaves from individual branches of "on" trees between FB + 92 and FB + 160, suggesting remobilization of resources, especially carbohydrates (Nzima, 1994) and nitrogenous compounds (Weinbaum et al., 1994). To our knowledge, our study is the first quantitative evidence of an immediate cost of fruiting on vegetative growth of pistachio sampled shoot organs. Relocation of stored assimilates and other metabolites from sources to organs requiring a large investment of energy have been reported in many plant species

(Dickson, 1989; Hansen, 1971; Hansen and Beck, 1990; Oliveira and Priestly, 1988; Wood and McMeans, 1981).

We compared dry matter accumulated per centimeter length of individual current-year and 1-year-old wood and used this measure to indicate growth in girth over a 2-year cycle because pistachio trees produce longer shoots during "on" than "off" years. The seasonal average total DMs increased 10- and 27- fold, respectively, among individual current wood of "on" and "off" trees, but the average total DMs of individual current wood of "on" trees were twice those of "off" trees (Table 1). Considering that individual current wood of "off" trees accumulated twice as much dry matter per centimeter length (grams per cm) as those of "on" trees (Fig. 3A) and yet the former were only one-fourth of the length, it can be concluded that current wood of "off" trees expanded twice as much as those of "on" trees. The rapid expansive growth of the short individual current wood of "off" trees was more than compensated for by the greater length of current wood of "on" trees insofar as the latter trees invested twice the average total dry matter into individual current wood (Table 1). The cost of fruiting on individual current wood of "on" trees was represented by DM losses of ≈0.30 g per shoot between FB + 130 and FB + 160 (Table 1) that coincided with rapid growth of nuts.

Individual 1-year-old wood of both "on" and "off" trees lost dry matter at the beginning of spring growth, suggesting a possible use of reserves during winter and for sustaining new growth before leaf photosynthetic competence (compare DMs at FB + 160 in Fig. 3A with those at FB + 10 in Fig. 3B). The slow growth recorded in individual 1-year-old wood of "on" trees (Fig. 3B) occurred coincidentally with increases in leaf area (Figs. 1 A and B), leaf DMs (Fig. 2A), current wood (Fig. 3A), rachises (Fig. 5), and nuts (Fig. 6B) and coincided with the abscision of 25% of the nuts (Fig. 6A) and the first wave of inflorescence bud abscission (Fig. 4A). There was, however, a 150% increase in DM per centimeter length of individual 1-year-old wood following the final abscission of nuts around FB + 60 (Fig. 4A) and another 14% decrease in DM between FB + 92 and FB + 148. These results clearly indicate the importance of individual 1-year-old wood in source–sink relationships that must be included in studies examining competition between vegetative and reproductive structures and alternate bearing in pistachio. Evidence of complex combinations of competition for resources among inflorescence buds, flowers, fruit, leaves, current and 1-year-old vegetative organs, and roots has been provided for *Betula pendular* Roth (Tuomi et al., 1982), *Catalpa speciosa* Warder ex Englem (Stephenson, 1983), olive (Rallo and Suarez, 1989), *Vigna unguiculata* L. Walp (Schulze et al., 1983), *Prunus persica* L. Batsch (peach) (Chandler, 1942; DeJong et al., 1987), sweet cherry (Kappel, 1991), and other plant species (Reekie and Bazzaz, 1987a, 1987b). "Off" pistachio trees invested 4.60 g of dry matter into individual 1-year-old wood between FB + 10 and FB + 160, whereas "on" trees initially invested 2.27 g of dry matter into similar organs between FB + 10 and FB + 92 but lost 0.94 g of this between FB + 92 and FB + 160 for an average total seasonal gain of 1.33 g (Table 1), equivalent to 33% of that of "off" trees. It is surmised that the cost of fruiting on individual 1-year-old wood was ≈0.94 g per shoot. These data suggest that pistachio trees invest 350% as much total dry matter into individual 1-year-old wood as into individual current wood during the "off" cycle compared with an investment of ≈61% as much dry matter into 1-year-old wood as into current wood during the "on" cycle. However, over a compete alternate-bearing cycle, the average total investment into vegetative shoots is similar because the dynamics of investment is counterbalanced by the storage role of the short 1-year-old wood.

Apparently, fruiting had immediate costs on individual shoot organs as measured by losses in DM between seasonal peak DMs and the subsequent lowest DM values. We recorded losses in average total DMs of individual leaves, current and 1-year-wood of "on" trees of 1.12%, 0.32%, 1.12%, and 1.04%, respectively, of the average total DMs of individual branches. This translated to losses of 5.68%, 5.87%, 26.72%, and 16.42% of the seasonal average peak DMs attained by the respective individual shoot organs. These data are at variance with the "trade-off" hypothesis that resources are invested in reproduction at the same rate that reproduction drains resources from somatic investment (Abrahamson, 1979; Reekie and Bazzaz, 1987b). We conclude that once pistachio seeds start developing in July, they become major sinks that draw resources from individual vegetative organs at rates greater than they are invested.

Using naturally "on" and "off" pistachio trees unmanipulated crops enabled us to identify the immediate and delayed costs of fruiting as well as the potential contribution by different components of the branch toward the development of the whole branch during alternate-bearing years. The initial rapid development of leaf area among "on" trees implied that these leaves became sources to other leaves and developing organs, whereas the slow leaf growth among "off" trees indicated delayed costs of fruiting of the previous heavy crop year. Individual 1-year-old wood played a major role as sources and sinks for developing current-year shoots, leaves, inflorescence buds, and nuts.

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