Fertilizer Nitrogen and Boron Uptake, Storage, and Allocation Vary during the Alternate-bearing Cycle in Pistachio Trees

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Abstract. The effects of alternate bearing on recovery and loss of isotonically labeled fertilizer N and B and on the accumulation of carbohydrate and N reserves were assessed in mature 'Kerman' pistachio *(Pistacia vera* L.) trees. Total recovery of labeled fertilizer N applied once (in late January) was ≈ 60% greater if applied to trees entering an "off" than an "on" year, with respect to fruiting. Eleven percent more labeled B was recovered in off- than on-year trees. Five times more N (1 vs. 0.2 kg N) was lost from the tree in fruit and senescent leaflets from on- than off-year trees. In dormant trees, 144% and 22% more starch and N reserves, respectively, were present after off than on years. Thus, on-year trees were characterized by a greater reproductive demand for N and carbohydrates, reduced accumulation of C and N (i.e., storage) reserves in perennial tree parts, and reduced recovery of January-applied labeled fertilizer N than off-year trees. As B is absorbed passively, the higher transpiration that may accompany the 43% larger leaf area per tree and the probability of increased root growth probably contributes to its increased uptake during off years. The enhanced labeled N recovery in early spring by trees entering their off year preceded fruit and seed development in on-year trees. The differential tree capacity for nutrient uptake in spring may have been conditioned the previous rather than the current year. The increased uptake of labeled N by trees entering an off year (i.e., emerging from an on year) was associated with lower levels of carbohydrate and N reserves than for on-year trees that had just completed an off year. Future experimentation should assess the comparative capacity for nutrient uptake by on-and off-year trees at other stages of phenology, e.g., during seed development and postharvest.

Alternate bearing-the alternation of high and low crop years—is widespread among commercially important tree fruit species (Monselise and Goldschmidt, 1982) including pistachio (Crane and Al-Shalan, 1977; Crane and Nelson, 1971, 1972; Crane et al., 1973, 1976; Johnson and Weinbaum, 1987; Takeda et al., 1980). Alternate-bearing studies have addressed a) horticultural means (via thinning, pruning) to regulate cropping and b) effects of crop load on vegetative growth, flowering, and the levels of carbohydrate and N reserves (Monselise and Goldschmidt, 1982). In contrast, the effect of alternate bearing on patterns of nutrient uptake and use have received scant attention.

Fruit photoassimilate only a small fraction of their C requirement (Bazzaz et al., 1979). Thus, fruit depend on photoassimilates produced elsewhere. Fruit development may be supported by current photoassimilation or by a redistribution of carbohydrate reserves (principally starch) in shoots, trunk, and roots (Goldschmidt and Golomb, 1982; Loescher et al., 1990; Tromp, 1983). Starch reserves are especially important in early spring before sufficient leaf expansion has taken place to support the net export of photoassimilates (Turgeon, 1989). After the leaves are fully expanded, fruit growth typically occurs at the expense of vegetative growth. The apparent order of priority for C among metabolic sinks is seeds > fleshy fruit parts = shoot apexes and leaves > cambium > roots > storage (Cannell, 1985; Goldschmidt and Golomb, 1982; Loescher et al., 1990).

Nitrogen uptake requires energy (Marschner, 1986; Salisbury and Ross, 1985) and N influx is independent of transpiration (Schulze and Bloom, 1984). Because roots compete poorly with fruit for assimilates (Cannell, 1985; Goldschmidt and Golomb, 1982; Head, 1969; Loescher et al., 1990; Maggs, 1963; Smith, 1976), a decrease in active nutrient uptake could be anticipated in heavily cropping trees. The impact of alternate bearing on nutrient uptake by trees needs to be assessed in light of increasing public concern over the relationship between fertilization and nitrate leaching, groundwater pollution, and the efficiency of fertilizer N use (Weinbaum et al., 1992). Carbohydrate deprivation in roots of heavily cropping trees may limit nitrate reduction (Minotti and Jackson, 1970) and uptake (Golomb and Goldschmidt, 1987; Oliveira and Priestley, 1988). Boron uptake is apparently passive, because reduced temperature and the addition of respiratory inhibitors had little effect on B uptake (Bingham, 1970). Uptake of passively absorbed nutrients is influenced by their concentration in the soil solution and the transpirational flux rate of the plant (Barber, 1984; Marschner, 1986).

The objectives of this study were to a) quantify the annual loss of N in fruit and leaf litter from mature, severely alternate-bearing 'Kerman' pistachio trees; b) determine whether alternate bearing influences tree capacity for N and B uptake and the efficiency of nutrient recovery using isotonically labeled N and B as tracers; and c) determine the impact of crop alternation on N and starch reserves in dormant trees.

Materials and Methods

Plant material and experimental manipulation. Six adjacent, 15-year-old on-year 'Kerman pistachio trees on *Pistacia atlantica* Desf. rootstock of uniform size were selected at the Wolfskill Experimental Orchard (Winters, Calif.) in 1984. Pistachio trees are highly entrained in California with respect to the alternate-bearing cycle (heavy cropping occurs in even-numbered years). Three of the six on trees were deflorated manually in April 1984 to generate

off trees under identical environmental conditions. On-year trees yielded an average 45 kg dry weight (DW) of fruit (hull, shell, and kernel) per tree. Some defloration in April kept off trees completely fruitless. We anticipated that such extreme differences in crop load would provide a sensitive experimental system for testing the influences of alternate bearing on levels of nonstructural carbohydrate and tree capacity for nutrient recovery. The cropping status of the two tree groups differed each year and switched the subsequent year (Table 1).

Effect of alternate bearing on leaflet count, area, and DW per tree. Pistachio leaves are pinnately compound and average five leaflets per leaf. The total number of leaflets per tree was counted each July. Total canopy leaf area and DW (determined after drying for 48 h at 60C) were estimated after a random path sampling each August (Jessen, 1955). Leaflet area was determined using an area meter (Delta-T; Decagon, Pullman, Wash.). Total leaflet areas per tree were calculated as the product of leaflet count and the average area per leaflet.

In 1988–90, five well-exposed spurs were removed from each tree to provide 15 observations at each of five periods for on- and off- year trees. Spurs were taken to the laboratory at the following times: bud swell (early April), mature distillate flowers (mid-April), the beginning of embryo enlargement (late June or early July), fruit maturity (September), and leaf abscission (November). After each sampling, leaflets were dried as previously described, and leaf DW per area (mg·cm^{-2}) was determined using the total leaflet DW and area per spur. Leaflets were stored for subsequent N analyses. Total leaflet DW per tree at each period was estimated to be the product of individual DW per area (average of five spurs per tree) and total leaflet area per tree. Leaf DW per area did not vary when spurs sampled along a random path were compared with spurs sampled at the tree periphery, presumably because the pistachio canopy is relatively open (data not presented).

Effect of alternate bearing on net annual N removal per tree in fruit and leaf litter and leaf N resorption per tree canopy. The amount of N loss per tree in senescent leaflets (leaf litter) and the harvested crop was determined in 1986-90. Tissue samples were oven-dried at 60C and ground to pass a 0.57-mm (30-mesh) screen before N analysis. Total N was determinedly a Kjeldahl procedure modified to include nitrate. To analyze labeled N, the ammonium salts were sent to Isotope Services, Los Alamos, N.M., where the ammonia was oxidized to N_2 gas before the isotopic composition was determined by mass spectrometry. Atomic percent values were expressed as percentage of N derived from fertilizer using standard conversions (Cabrera and Kissel, 1989; Hauck and Bremner, 1976). The product of total leaflet count per tree, average leaflet DW, and N concentration at leaf abscission (as discussed previously) was used to estimate the quantity of N carried to the

orchard floor in leaf litter from each of the six trees.

Each on tree was harvested individually and the crop was weighed. Fruit subsamples ($\approx$100 fruit/tree) included marketable fruit (fully developed seed, dehisced shell, and loosened hull), blank fruit (parthenocarpic fruit and fruit with aborted seed), and fruit with shriveled, discolored hulls. Marketable fruit comprised 60% to 70% of the total harvest weight but contained 85% ± 2% of the N in the crop (data not shown). Total N removal by the harvested fruit was determined as the product of total dry matter yield and N concentration.

Net leaflet N resorption per tree canopy was calculated in 1990 as the difference between the total N content of the foliage between fruit and seed maturation (early September) and natural leaflet abscission in mid-November. Thus, net leaf N resorption equals the product of total leaflet DW per tree and the difference in leaf N concentration over the selected interval.

Effect of alternate bearing on the recovery of soil-applied labeled N and B. Isotopic N was supplied to each of the three off- and three on-year trees as a 40% solution (w/v) of ^{15}N-depleted $(NH_4)_2SO_4$ on 26 Jan. 1987. The solution was applied at 1.5 kg N/ tree in concentric trenches 25 cm deep, 1.2 and 1.8 m from the trunk. The trenches were covered with soil to minimize ammonia volatilization. Leaflet and fruit samples were collected and processed as above before determining the amount of labeled N removed during 1987–90. After labeled N was applied, trees were fertilized annually in 1988–90 with nonlabeled N at the same rate.

On 11 Apr. 1990, isotopic B was applied in a single circular trench $\approx$1 m from the trunks at 3.3 g B/tree as undissolved, ^{10}B-enriched boric acid [95.91 atom% ^{10}B (Eagle Picher Specialty Products, Quapaw, Okla.)] and the trees were irrigated immediately thereafter. Tissue samples were dried and ground to pass a 30-mesh screen, and 0.5-g subsamples were ashed at 500C for 8 h and extracted with 1 N HNO_3. Total B was determined using the azomethine method (Wolf, 1971), and labeled B (Hanson, 1991) was determined using an inductively-coupled plasma mass spectrometer (Sciex 500; Perkin Elmer, Norwalk, Corm.). A certified isotopic solution (National Institute of Standards and Technology) was used to ensure the accuracy of sample isotopic ratios. Isotopic ratios for unfertilized tissue were obtained from leaf samples collected on 11 Apr. As described for N, leaflet and fruit samples (at harvest) were analyzed to determine total and labeled B quantities.

Dormant tree excavation and analyses. On 15 Jan. 1991, each tree was excavated and fractionated into roots, 1-year-old (current) wood, trunks, and remaining (canopy) branches. After fresh weights were recorded, the various tree fractions were mechanically chipped. Chipped subsamples were weighed fresh and reweighed after oven drying to constant weight (150 to 250 g) to calculate total DWs of

Table 1. Summary of experimental details for six adjacent, mature 'Kerman' pistachio trees between April 1984 and January 1991.

Tree group	Tree cropping status							
	1984[z]	1985	1986	1987[y]	1988[x]	1989[x]	1990[x,w]	1991[v]
A	Off	On	Off	On	Off	On	Off	On
B	On	Off	On	Off	On	Off	On	Off

[z]Group A trees were deflorated in April 1984 to generate off-year trees.
[y]All trees were fertilized with labeled N on 26 Jan. 1987.
[x]All trees were fertilized annually with nonlabeled fertilizer N.
[w]All trees were fertilized with labeled B on 11 Apr. 1990. Group A trees were fertilized with labeled N in their on year and with labeled B in their off year. The opposite was true of Group B trees.
[v]All six trees were excavated on 15 Jan. 1991, fractionated into various tree parts, weighed, and analyzed for nutrients and nonstructural carbohydrates.

the various tree fractions. The chipped material was ground to pass a 30-mesh screen, and 1-g subsamples were used to determine total N, labeled N, total B, and labeled B. Total labeled N and B recovery was based on the sum of the quantities of labeled N and B in fruit and senescent leaflets from the time of label application (1987 for N and 1990 for B) and the residual label in perennial, woody organs (determined after tree excavation in January 1991).

Carbohydrate analyses and effect of alternate bearing on starch content and percentage distribution in dormant trees. Subsamples (0.3 to 0.5 g) of the various dormant tree fractions were extracted once for glucose and sucrose (10 min each) in boiling, 80% ethanol. Starch was hydrolyzed from the ethanol-insoluble material after a 90-min incubation at 55C (Na-acetate buffer, pH 4.8) with amyloglucosidase (grade 2; Sigma, St. Louis). Sugar and starch concentrations (after hydrolysis) were determined using standard enzymatic methods as outlined by Sturgeon (1990). Total tree carbohydrates were calculated using total organ DWs and their corresponding concentrations. One-way analyses of variance were performed using Statview 2 (Abacus Concepts, Berkeley, Calif.).

Results

Effect of alternate bearing on vegetative growth as indicated by leaflet number, total leaflet area, and leaflet DW per tree. The DW of terminal (vegetative) buds in on- and off-year trees were similar (Table 2). Total N concentration in buds at budbreak was higher in off- than on-year trees, but N content per bud did not differ between on- and off-year trees. In contrast, 1 week later (13 Apr.) when pistillate flowers were mature, the leaf mass and leaf N content per shoot were greater in off- than on-year trees (Table 2). Total leaflet counts, areas, and DWs per tree for off trees averaged 20%, 43%, and 44% more leaflets, total leaflet area, and leaflet DW, respectively, per tree than on trees in 1988–90 (Table 3). Average leaflet area and DW were also greater in off- than in on-year trees, although these differences were not significant at *P <0.05.* Total leaflet area per tree was >50% larger in 1989 (tree group B) when they were off than in 1988 when they were on (Table 3). In contrast, leaf area per tree in 1989 was reduced 30% in trees that were off in 1988 (tree group A) than when they were on. Similar changes in leaflet counts and leaflet DWs per tree were also observed (Table 3).

Table 2. Dry weight (DW), N concentration, and early spring recovery of labeled N in terminal vegetative buds at budbreak (7 Apr. 1987) and immature leaves (13 Apr. 1987) after labeled N was applied (26 Jan. 1987) to on- and off-year trees.

Organ	Tree cropping status[z] (1987)	DW	N (%)	N content	NDLF[y] (%)	Labeled N
		(g/bud)		(g/bud)		(mg/bud)
Buds (7 Apr.)	On	0.74[w]	4.69	0.034	0.15	49.7
	Off	0.66	5.05	0.033	0.29	95.3
		NS	*	NS	NS	NS
		(g/spur)		(g/spur)		(mg/spur)
Leaves (13 Apr.)	On	0.91	5.16	0.047	2.31	1.09
	Off	2.38	4.57	0.108	5.40	5.84
		****	**	****	**	**

[z]Off-year trees in 1987 cropped heavily in 1986 and vice versa.
[y]Nitrogen derived from labeled fertilizer, expressed as a percentage of total N.
[w]Each value is the mean of three tree replications.
[NS,*,**,****]Nonsignificant at $P \le 0.05$ or significant at $P \le 0.05$, 0.01, or 0.0001, according to F test.

Table 3. Use of random path sampling (August) and total tree leaflet counts to determine the effect of alternate bearing on average leaflet area (LA), dry weight (DW), DW per LA, leaflet DW per tree, and LA per tree over 3 years.[z]

Cropping status	Tree group	Year	Leaflet averages			Leaflet totals/tree		
			LA (cm^2)	DW (mg)	DW/LA (mg·cm^{-2})	Count (1000s)	LA[y] (m^2)	DW[x] (kg)
Off	A	1988	35.9	524	14.6	39.09	140	20.4
	B	1989	29.6	437	14.7	56.82	167	24.5
	A	1990	31.8	447	13.8	54.93	173	24.1
		Mean	32.4	469	14.4	50.28	160	23.0
On	B	1988	33.1	480	14.5	32.98	109	15.8
	A	1989	23.3	332	14.1	40.94	95	14.2
	B	1990	25.1	343	13.6	53.30	133	18.1
		Mean	27.2	385	14.1	42.40	112	16.0
			NS	NS	NS	NS	*	**
Off : on ratio			1.19	1.2	1.02	1.19	1.43	1.44

[z]Each value is the mean of three tree replications.
[y]Calculated as the product of leaflet count per tree and average LA (the latter obtained by random path sampling in August).
[x]Calculated as the product of total leaflet count per tree and average DW per leaflet.
[NS,*,**]Nonsignificant at $P \le 0.05$ or significant at $P \le 0.05$ or 0.01, respectively, according to F test.

Effect of alternate bearing on leaf N resorption and N removal per tree in harvested fruit and leaf litter. Nitrogen removal associated with the loss of above-ground annual organs (i.e., mature fruit plus senescent leaflets of on-year trees averaged 400% more (1.0 vs. 0.2 kg N/tree) than off-year trees (Fig. 1). The N
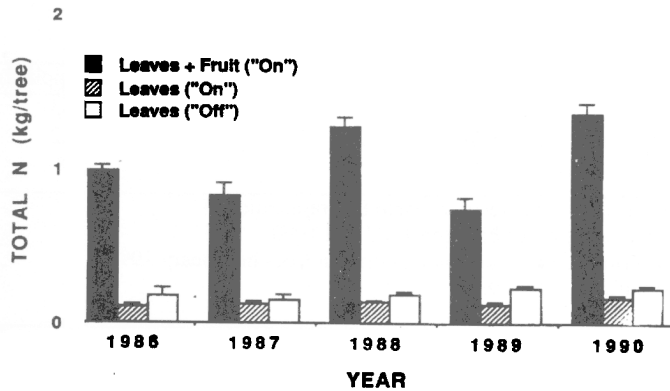
content of leaf litter *(20 Nov.)* in on-year trees averaged 15% less than off-year (fruitless) trees in 1990 (Table 4). This difference resulted from a somewhat greater area per leaflet and higher leaflet counts in off-year trees (Table 3).

Our calculations indicated that there was $\approx 50\%$ more N in the leaflets of off- than on-year trees (530 vs.310 g, Table 4) in early July. The decrease in leaflet N concentration between 2 July and 10 Sept. was more conspicuous in on-than off-year trees, presumably because of seed demand for N in the former. Sixty percent to 70% net leaflet N resorption occurred between early July and natural leaf fall in November when calculated based on leaflet N concentration (calculations based on data in Table 4). The percentage of leaflet N resorption did not seem to vary consistently between off- and on-year trees (data not shown).

Effect of altenate bearing on the amounts and distribution of DW, N, and starch. Total tree DWs did not differ after on or off years (Table 5). The canopy (branches) constituted nearly 70% of tree DW followed by roots, trunk, and current wood (1990 shoot growth). Dormant canopy branches contained nearly 60% of the total tree N content in on- and off-year trees (Table 5). Off_{1990} trees (i.e., trees analyzed during the dormant season after their off year) contained *22%* more total N in perennial organs than on_{1990} trees (Table 5).

Fig. 1. Annual removal of total N in senescent leaflets and harvested fruit of mature 'Kerman' pistachio trees. Each value is the mean ±SE of three tree replications.

Table 4. Effect of alternate bearing on leaflet N concentration, leaflet N content per tree,[z] and net leaflet N resorption per tree between fruit maturation (10 Sept.) and natural leaf fall (20 Nov.).

	Sampling stages and dates						
	Preseed fill (2 July)		Fruit maturation (10 Sept.)		Leaf fall (20 Nov.)		
	Leaflet N						
Cropping status 1990	Concn (% dry wt)	Content (g/tree)	Concn (% dry wt)	Content (g/tree)	Concn (% dry wt)	Content[y] (g/tree)	Net resorption (g/tree)[x]
Off	2.56[w]	530	2.45	586	0.97	192	394
On	2.39	310	2.03	287	0.97	164	123
	NS	***	*	***	NS	*	

[z]Leaflet N content (g/tree) was calculated using leaflet N concentrations and leaflet biomass per tree (Table 2) determined in early July (preseed fill), early September (harvest), and mid-November (leaf fall).
[y]Because leaflets were sampled just before natural leaf fall, these values are considered to represent the N carried to the orchard floor in leaf litter.
[x]Calculated as the difference between leaflet N content on 10 Sept. and 20 Nov.
[w]Each value is the mean of three tree replications.
[NS,*,**,***]Nonsignificant at $P \leq 0.05$ or significant at $P < 0.05$, 0.01, or 0.001, respectively, according to F test.

Table 5. Effect of tree cropping status in 1990 (on or off) on tree dry weight and N and starch content and percentage distribution in mature, dormant 'Kerman' pistachio trees in January 1991.[z]

Variable	Current wood		Canopy		Trunk		Roots		Tree total	
	On	Off	On	Off	On	Off	On	Off	On	Off
Dry weight (kg/tree)	3.4	4.9	248.1	35.0	47.3	38.2	59.5	73.3	358.2	351.3
	***		NS		NS		NS		NS	
N content (g/tree)	40	71	1118	1327	117	108	606	782	1881	2287
	***		NS		NS		NS		**	
N distribution (% of total)	2.2	3.1	59.4	57.9	6.2	4.7	32.2	34.4	100	100
	NS		NS		*		NS			
Starch content (g/tree)	35	24	402	3048	189	420	2721	4684	3348	8176
	NS		***		NS		**		***	
Starch distribution (% of total)	1.1	0.3	12.4	37.4	5.7	5.1	80.8	57.2		
	NS		***		NS		**			

[z]Each value is the mean of three tree replications.
[y]Data are characteristic of trees excavated in mid-January; thus, trees had a higher starch content after an off (1990) than an on year. However, because the on year follows an off year, on-year trees start their season with greater reserves than off-year trees.
[NS,**,***]Nonsignificant at $P \leq 0.05$ or significant at $P \leq 0.01$ or 0.001, respectively, according to F test.

There were lower starch concentrations in perennial organs of dormant trees after on than off years. Starch constituted >80% of the total nonstructural carbohydrate content in woody organs, and there were no differences between on$_{1990}$ and off$_{1990}$ trees in glucose and sucrose concentration or content (data not presented). Tree starch content averaged 144% higher after off$_{1990}$ years than on$_{1990}$ years (e.g., ≈8.2 vs. 3.3 kg total starch/tree, respectively). Similar differences in evergreen fruit tree species have been reported (Goldschmidt and Golomb, 1982; Jones et al., 1975; Smith, 1976).

Starch distribution varied between on- and off-year trees. During dormancy after their on year, trees contained 81% of total tree starch in their roots, whereas, the roots contained only 57% of total tree starch during dormancy after their off year (Table 5).

Alternate bearing and tree recovery of isotonically labeled N and B. When spring growth resumed, 2.5 months after labeled N application, the expanding terminal buds in off-year trees tended to accumulate more labeled N per bud than corresponding buds in on-year trees (Table 2). This tendency, apparent on 7 Apr. 1987, was strengthened over the next week when off-year trees contained five times as much labeled N in leaves per shoot than on-year trees. There was more labeled N in the leaves of off- than on-year trees and the percentage of leaf N derived from recently applied labeled fertilizer was significantly higher in the off- than on-year trees (Table 2).

Trees entering an off year when labeled N was applied recovered 76% more labeled N in senescent leaflets and fruit over 4 years (two alternate-bearing cycles) than trees fertilized with labeled N at the beginning of their on year (566 vs. 321 g/tree, respectively; Table 6). Fruit accounted for 70% to 75% of the labeled N removed in annual organs in 1987–90 (data not presented).

When trees were excavated (January 1991), canopy branches contained the most labeled N, followed by roots, trunks, and current wood (Fig. 2). After 4 seasons, off$_{1987}$ trees contained >75% more labeled N in perennial tree parts than on$_{1987}$ trees (Fig. 2, Table 6) and had higher labeled N (LN) to total N (TN) ratios in all perennial organs [≈ 7% to 13% of LN: TN in off$_{1987}$ trees compared with 5% to 8% LN: TN for on$_{1987}$ trees (data not shown)].

Total labeled N recovery was 59% higher in off$_{1987}$ than in on$_{1987}$ trees. That is, applying labeled N to trees entering an on year in late January resulted in ≈33% labeled N recovery, while applying labeled N to noncropping, off-year trees resulted in >50% labeled N recovery over 4 years (Table 6).

Labeled B recovery in perennial organs, leaflets, and fruit was <90 mg/tree, or <3% of the quantity applied (3.3 g). Labeled B in leaflets at harvest represented ≈ 40% (on$_{1990}$) to 50% (off$_{1990}$) of entire tree totals after one season (Fig. 3). Labeled B removal in petioles was <39% of that in leaflets and is included in tree totals. Whereas labeled N removal by leaflets of on-year trees in 1987 was only 19% the amount of labeled N in fruit, leaflets of on$_{1990}$ trees contained 2.7 times more labeled B than fruit in 1990. Fruit N concentrations (typically ≈27% to 2.5% of combined hull, shell, and kernel DW at maturity) were of the same order of magnitude as those in leaflets, but fruit B concentrations (weighted average of all fruit portions) were only 57% to 10% of leaflet B concentrations. This response is the result of an extreme difference between fruit and leaves in the demand or allocation of N and B.

The labeled B content of roots was 71% greater in the off$_{1990}$ than on$_{1990}$ trees (Fig. 3). However, in current wood, canopy, and trunk portions, the quantity of labeled B did not differ greatly between on- and off-year trees. The labeled B concentration was highest in roots (2.4% to 3.2% of total B), followed by 1990 shoot growth (current wood) (1.5%), and canopy branches and trunk (0.7% to 0.8%; data not presented). Total labeled B recovery in all tree

Table 6. Total amount and percentage recovery of the labeled fertilizer N applied to mature cropping (on-year) and fruitless (off-year) 'Kerman' pistachio trees in January 1987.[z]

| Cropping status (1987) | Labeled N recovery | | | |
| | Senescent leaflets + fruit[y] (g/tree) | Woody organs[x] (g/tree) | Total | |
			(g/tree)	(% of applied)
On$_{1987}$	321	121	422	33
Off$_{1987}$	566	216	793	52
	*	*	*	*

[z]Each value is the mean of three tree replications.
[y]Cumulative totals between 1987 and 1990.
[x]Determined after excavating dormant trees in January 1991.
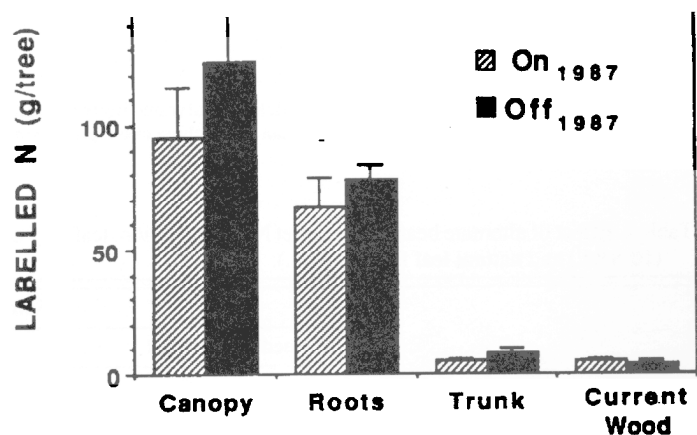*Significant at $P \leq 0.05$.

Fig. 2. Recovery of labeled N, applied 26 Jan. 1987, in perennial parts of mature 'Kerman' pistachio trees after tree excavation on 15 Jan. 1991. On$_{1987}$, trees were on and off$_{1987}$ trees were off during 1987, the year that labeled N was applied. Each value is the mean ±SE of three tree replications.
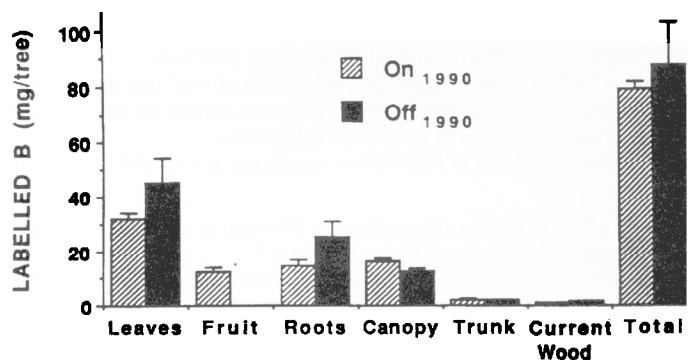

Fig. 3. Recovery of labeled B, applied 11 Apr. 1990, by mature 'Kerman' pistachio trees. Off$_{1990}$ and on$_{1990}$ refer to tree cropping status in 1990. Each value is the mean ±SE of three tree replications.

tissues was 11% greater in off$_{1990}$ than in on$_{1990}$ trees during the year labeled B was applied. The likelihood of greater transpiration by off than on-year trees (off trees have a 43% greater transpiring leaf surface area, Table 3) may have caused the 11% increase in labeled B uptake, although the exact importance of this factor can not be determined without measuring tree water use and considering soil B supply characteristics. As a percentage of applied label, 2.7% and 2.4% were recovered by off$_{1990}$ and on$_{1990}$ trees, respectively. This finding is consistent with that of labeled N recovery totals,

even though Group A trees were fertilized with labeled N in their on year in 1987 and with labeled B in their off year in 1990 (Table 1) and vice versa. Of the three replicate off$_{1990}$ trees, one contained noticeably less DW in canopy leaves in 1990 (60% of the remaining replications than the others). This response resulted in 48% less labeled B recovery than the average of the other two trees. We estimate that the total labeled B recovery of off$_{1990}$ trees would have been 29% greater than on$_{1990}$ trees if the atypical replicate had been discarded.

The within-tree total B distribution differed considerably from that of labeled B. Canopy branches of off$_{1990}$ and on$_{1990}$ trees contained 61% and 69%, respectively, of total tree B in perennial organs (data not shown), but roots off$_{1990}$ and on$_{1990}$ trees contained 60% and 42%, respectively, of total labeled B (Fig. 3). This difference may indicate that recently absorbed B is sequestered in roots after uptake and is redistributed later to other parts of the tree. Because most B is thought to be in cell walls and associated with sugar and phenolic compounds with cis-diol hydroxyl groupings (Dugger, 1983), any cropping effect on the relative proportions of these compounds in roots could influence B binding. The availability of B complexation sites could influence B uptake.

Discussion

Woody perennials differ from herbaceous annual species in ways other than longevity and the production of secondary vascular tissue. Much documentation supports the concept that tree experiences in the current year, such as crop load and drought, influence tree performance in subsequent years. Alternate bearing gives testimony to the reality of carryover effects. That is, heavy cropping (the on year) is linked functionally with the midsummer abscission of inflorescence buds and conditions the tree to enter the subsequent year with relatively few inflorescences and, as a result, experience an off year (Crane and Nelson, 1971). Trees entering their on year (having just experienced an off year) have greater overwinter carbohydrate and N reserves (Table 4) than trees entering their off year. One manifestation of greater tree reserves entering an on year is longer, early season (April to mid-May) shoot extension than is characteristic of off-year trees (i.e., trees with lower reserves, coming off of an on year) (Crane and A1-Shalan, 1977).

We hypothesized that nutrient uptake would be resource-limited in on-year trees. That is, the dominance of fruit as a metabolic sink would limit a) carbohydrate transport to roots, b) root growth, and c) energy-dependent nutrient uptake. Although our data substantiated reduced labeled N recovery (applied in late January) by on-relative to off-year trees (Table 6), our interpretation of the phenomenon is less clear. Greater labeled N recovery in spring by off-year trees (Table 6) occurred despite reduced carbohydrate and N reserves relative to trees entering their on year (Table 5). Thus, reduced carbohydrate and N reserves did not seem to limit early season labeled N uptake relative to trees entering their on year. Differences between on- and off-year trees in starch content may have been even greater during seed fill, the period of maximum resource demand by the fruit. The greater recovery by off-year trees of labeled fertilizer N applied during late January cannot be ascribed to the negative impact of current-year fruit development on root growth and activity because the enhanced labeled N uptake by off- relative to on-year trees preceded the significant period of fruit and seed development in on-year trees. More likely, the greater spring labeled N recovery by off-year trees, i.e., after on years, was conditioned previously, i.e., during the on year. To our knowledge, this is the first report of the impact of alternate bearing on the capacity for nutrient uptake by mature, field-grown trees.

Starch concentrations of various tree parts are frequently reported (Crane and A1-Shalan, 1977), but few studies have addressed the size, i.e., the content, of the nonstructural carbohydrate pool in mature trees (Goldschmidt and Golomb, 1982; Murneek, 1942). The starch content of mature dormant pistachio trees was ≈2.5 times larger after an off than an on year (8.2 vs. 3.3 kg/tree, respectively). The availability of a larger pool of metabolic reserves in trees that recently completed an off year (and are entering anon year) may be an integral part of the alternate-bearing cycle.

Although our data are not sufficient to develop a C budget for off- vs. on-year pistachio trees, an estimated removal of 20 kg C/tree in the fruit of on-year trees (45 kg DW of fruit per tree multiplied by an estimated 45% C per unit DW) coupled with a reduced leaf area per tree averaging 43% (Table 3) is consistent with the imbalance between C demand and relative capacity for C assimilation in on-year trees.

Trees analyzed during the dormant season after their off year contained 22% more total N in perennial organs than trees after their on year. Presumably, the greater tree N content includes a greater amount of storage N that accumulates in late summer and fall as a result of soil N uptake and leaf N resorption (Millard and Neilsen, 1989; Millard and Roe, 1992; Millard and Thomson, 1989; Taylor, 1967) and is cycled into new growth the following spring. Thus, the larger accumulation of storage N in off-year pistachio trees may be considered an N buffer for use during on years (0' Kennedy and Titus, 1979) when N use by annual organs (fruit and leaf litter) is four times greater than it is in off years (Fig. 1). This conspicuously greater removal of N in annual organs of on-year trees was accompanied by a 37% lower recovery of soil-applied, labeled fertilizer N (Table 6) and ≈45% less leaf N resorption per tree (Table 6). Off-year trees recovered ≈350 g more of soil-applied, labeled fertilizer N than on-year trees (Table 6). Also, the greater leaf biomass in off-year trees (Table 4) was associated with an estimated 270 g (394 vs. 123 g/tree) higher net leaf N resorption than in on-year trees (Table 4). Decreases in leaf N concentration and N mass per unit leaf area during leaf senescence have been well documented (Chabot and Hicks, 1982; Spencer and Titus, 1972; Titus and Kang, 1982), but no studies have attempted to estimate the relative contribution of leaf N resorption to the entire within-tree pool of storage N. The greater net leaf N resorption (270 g N/tree in 1990) in off- than on-year trees (Table 4) accounts for >60% of the difference in total tree N content (406 g; Table 5) measured after tree excavation in January 1991.

The use of isotonically labeled fertilizer N allowed us to measure fertilizer N recovery directly. Although the fate of labeled fertilizer N not recovered by the trees was not determined, an inverse relationship between tree labeled N recovery and the likelihood of loss (leaching, denitrification) is anticipated.

Fertilizer N use efficiency (NUE) has been defined as the amount of fertilizer N recovered by the plant divided by the total amount of fertilizer N applied. NUE values between 25% and 50% are considered typical for crop plants (Weinbaum et al., 1992). Site-specific soil and climatic variables and fertilizer and irrigation application methods and rates influence NUE. Our data indicate convincingly that alternate bearing influences a tree's capacity to recover fertilizer N and, thus, its NUE. Off-year 'Kerman' pistachio trees recovered nearly 60% more labeled fertilizer N than on-year trees (782 vs. 493 g, Table 6). The relative difference in fertilizer N recovery between on- and off-year trees reported in this study is probably more significant than the absolute percentages of labeled fertilizer N recovery, which are influenced by site-specific,

management, and environmental variables (Weinbaum et al., 1992; Yamaguchi, 1991).

The apparent recovery of fertilizer N by plants is typically lower when isotonically labeled N is used (the direct method) than when the indirect or difference method is used (Jansson and Persson, 1982; Jenkinson et al., 1985). That is, labeled fertilizer N recovery by plants is less than the difference in N content between unfertilized and fertilized plants. Jenkinson et al. (1985) suggested that applying fertilizer N stimulates a net rnineralization of soil N, with subsequent consumption of the mineralized N by the crop-the so-called "priming" effect. Another explanation is that labeled fertilizer N will be immobilized in the organic soil N fraction when nontagged soil N is mineralized. By taking up isotonically diluted pool N, the plant will contain less tagged N and more nontagged N (Jansson and Persson, 1982; Jenkinson et al., 1985).

Fertilizer N recovery seemed to occur primarily during the year (and perhaps within several months) of fertilizer application, with very little influx of labeled N in subsequent years. Immobilization of labeled N in soil N pools that are not accessible to tree roots for uptake, N losses by leaching, denitrification, or both, and dilution of labeled N in soluble soil N pools resulting from the annual application of nonlabeled fertilizer N (Weinbaum et al., 1987) may contribute. Field-crop studies also indicate that, although 20% to 40% of the fertilizer applied may remain in the field after a single cropping, recovery of that residual fertilizer N in the soil by subsequent crops is estimated to be only 3% to 4% of the amount applied initially (Yamaguchi, 1991). Thus, to expect significant fertilizer N recovery by trees in subsequent years seems unwarranted, and trees should not be fertilized when their nutrient uptake capacity is limited. More detailed studies are needed, however, to determine how changes in nutrient uptake capacity vary over the alternate-bearing cycle. We do not know, for example, how the capacity for fertilizer N uptake varies during specific periods; i.e., preseed fill, seed fill, and postharvest, in on years.

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31