

Macronutrient Allocation to Leaves and Fruit of Mature, Alternate-bearing Pistachio Trees: Magnitude and Seasonal Patterns at the Whole-canopy Level

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ABSTRACT. Estimates of leaflet and fruit macronutrient (N, P, K, Ca, and Mg) accumulation and resorption were developed in six (three heavily cropping, on-year and three noncropping, off-year) mature pistachio (*Pistacia vera* L. ‘Kerman’) trees over three growing seasons during three stages of phenology [the spring growth flush (April to June); seed fill (late June to September); and leaf senescence (September to November)]. Crop load influenced total nutrient content per tree in annual organs (leaves and fruit), the relative allocation of nutrients between leaves and fruit, temporal patterns of nutrient accumulation in annual organs, and the magnitude of net leaf nutrient resorption per tree prior to leaf fall. In off-year trees, macronutrient accumulation in annual organs (leaves) was concentrated during the spring flush of growth. In contrast, significant macronutrient accumulation in annual organs of on-year trees (leaves plus fruit) occurred not only during the spring flush of growth but also during seed fill. Duration and magnitude of macronutrient accumulation were greater in on-year vs. off-year trees. Fruit N and P demand during seed fill was partially met by a net decrease in the N and P contents of the pericarp. These decreases in pericarp nutrient content during seed fill were equivalent to 32% and 26% of embryo accumulation of N and P, respectively. Fruit demand for N, P, and K during the spring flush of “on” years was accompanied by reduced leaf N, P, and K contents per tree. Net leaf N, Ca, and Mg resorption per tree during leaf senescence differed with crop load. Net leaf N resorption was significantly greater in off-year trees than on-year trees. Leaf N resorption presumably represents an important component of the N pool stored in perennial tree parts during dormancy. The greater leaf N resorption following “off” years was a function of greater leaf N concentration and greater leaf biomass per tree. In contrast, net leaf resorption of Ca and Mg was greater in on-year vs. off-year trees. Experimental validation of the magnitude and periodicity of nutrient uptake by mature pistachio trees is needed during the alternate-bearing cycle, especially in light of the potential contribution of current fertilization practices to groundwater contamination.

Although alternate bearing is common among fruit tree species, its impact on mineral nutrient uptake and allocation patterns has received little attention (Monselise and Goldschmidt, 1982). *Pistacia vera* L. (pistachio) is a severely alternate-bearing deciduous tree species (Crane and Iwakiri, 1981), with yields varying 3- to 5-fold between the heavily cropping “on” years and lightly cropping “off” years (Johnson and Weinbaum, 1987). This differential crop load is accompanied by a 30% reduction in leaf area per tree in “on” years (Weinbaum et al., 1994b).

In pistachio, budbreak, shoot elongation, and leaf expansion occur during the spring flush of growth between late March and mid-May (Crane and Iwakiri, 1981). Anthesis in California occurs in early April, and fruit growth can be separated into three distinct phases (Crane and Iwakiri, 1981): a) growth of the pericarp (April to mid-May); b) lignification of the endocarp (mid-May to June); and c) seed fill. Seed fill is concentrated over a 6-week period during which the embryo (barely visible macroscopically in mid-June) reaches full size by late July. Given this scenario, the question arises as to how the periodicity and magnitude of the demand for mineral nutrients vary over the alternate-bearing cycle.

In prune, fruit plus leaves may contain over 60% of the tree content of N and K (Weinbaum et al., 1994c). Thus, the growth kinetics of these organs likely indicate the magnitude of tree

nutrient demand and temporal nutrient allocation patterns during the growing season. The early season C and N demand of fruit and leaves may be met, in part, by redistribution from storage pools in perennial tree organs (Brown et al., 1995; Millard, 1995; Oland, 1959; Stassen et al., 1981; Taylor, 1967; Titus and Kang, 1982; Tromp, 1983; Weinbaum et al., 1994b). Later in the season, developing fruit may draw on labile nutrient pools in presenescent leaves (Niederholzer et al., 1991; Sparks, 1977; Weinbaum, 1988; Weinbaum et al., 1994c). The extent and specificity of leaf nutrient resorption coincident with fruit development may vary with species, crop load, and soil nutrient availability (Niederholzer et al., 1991; Sparks, 1977; Weinbaum, 1988).

Currently, fertilization practices in California pistachio orchards have ignored the possibility that nutrient demands and tree capacity for nutrient uptake from the soil vary with crop load over the alternate-bearing cycle (Brown et al., 1995; Weinbaum et al., 1994b).

Our objectives were to a) estimate the total seasonal macronutrient allocation to fruit and leaves of mature pistachio trees over the alternate-bearing cycle; b) evaluate the temporal patterns of macronutrient accumulation in these organs; and c) quantify leaf resorption of macronutrients. Our intent is to use these data to propose for further testing, a fertilization regime that reflects the biology of the pistachio tree over the alternate-bearing cycle.

Materials and Methods

CULTURAL CONDITIONS. Six adjacent, mature ‘Kerman’ trees on *P. atlantica* Desf. seedling rootstocks were selected in the Wolfskill

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Experimental Orchard at Winters, Calif. In April 1984, all flowers in three of the six on-year trees (three trees chosen at random) were removed by hand to generate a group of three off-year trees. Subsequent to the 1984 season, there were three off-year and three on-year trees each year, which alternated annually until the end of the study in 1990. Some flower removal was necessary in April of each season to ensure that off-year trees produced no fruit. During the period of this study, (1988–90), tree age increased from 19 to 21 years, and the average total fruit yield during “on” years ranged from 27 to 58 kg fruit per tree (total dry weight of all fruit portions). The fertilization schedule and cropping patterns have been reported previously (Weinbaum et al., 1994b).

ESTIMATION OF TOTAL LEAFLET NUMBER, AREA, AND DRY WEIGHT PER TREE; SEASONAL FRUIT WEIGHT; AND TISSUE SAMPLING PROCEDURE. Leaflet number per tree was counted during each July following cessation of shoot growth and leaf expansion (1988–90). Average area per leaflet was estimated in August using the random path procedure described by Jessen (1955). The area of about 100 leaflets on the randomly selected branch was measured using a Delta-T area meter (Decagon Inc., Pullman, Wash.). Total leaflet area per tree was then estimated as the product of the leaflet count per tree and the average area per leaflet.

Five branches were sampled (excised) from the outer periphery of each canopy to include 2-year-old wood, 1-year-old (current) wood, fruit (on-year trees only), and leaves. Samples were collected at the following times: the beginning of macroscopic embryo development (late June or early July), fruit and embryo maturity (September), and leaf abscission (November). Several weeks before leaf abscission, branches were enclosed in nylon mesh bags to retain senescing leaves following nutrient resorption. Leaflets were dried at 60 °C for 24 h, and specific leaflet weight [leaf weight (LW) per unit area (A)] was calculated using the total leaflet dry weight and area per branch. The LW/A values of five branches per tree were pooled for the tree average, providing a total of 15 observations at each period for on-year and off-year tree groups. These leaflets were saved for nutrient analyses (see below), which were expressed on a unit dry matter basis and as the amount per unit of leaflet area. Nutrient analyses were not made for 1- and 2-year-old wood.

The product of LW/A (at the time of sampling) and total leaflet area per tree was used to estimate total leaf dry weight per tree at each sampling period. Comparisons between branches sampled using the random path method and branches sampled at the periphery of the canopy showed no differences in LW/A, likely because the pistachio canopy is relatively open (Weinbaum et al., 1994b).

At the onset of seed fill and at fruit and embryo maturity (first and second branch samplings, respectively), all fruit per sampled branch of on-year trees were separated into their components. For the first sampling period (late June or early July), fruit were divided into a) immature embryos and b) a combined endocarp (shell) plus exocarp and mesocarp (hull) sample. At this stage, the endocarp and mesocarp of pistachio fruit are fused and physically inseparable. Mature fruit (obtained from branches sampled in September) were divided into mature embryo, endocarp, and combined mesocarp and exocarp. After thoroughly drying all components at 60 °C, the dry weights per fruit of each fruit portion were obtained, and the tissues were saved for nutrient analyses (see below).

In September, on-year trees were harvested (individually) just after the second branch sampling, and the total crop fresh weight was recorded. A fruit subsample (about 100 fruit per tree) was also weighed fresh, then subdivided into in-shell marketable fruit (fully developed embryo, dehiscent shell, and loosened hull), and nonmarketable fruit (fruit with aborted embryos or discolored

pericarps). Fruit subsamples were then processed, dried, and reweighed. Marketable fruit comprised 60% to 70% of the total

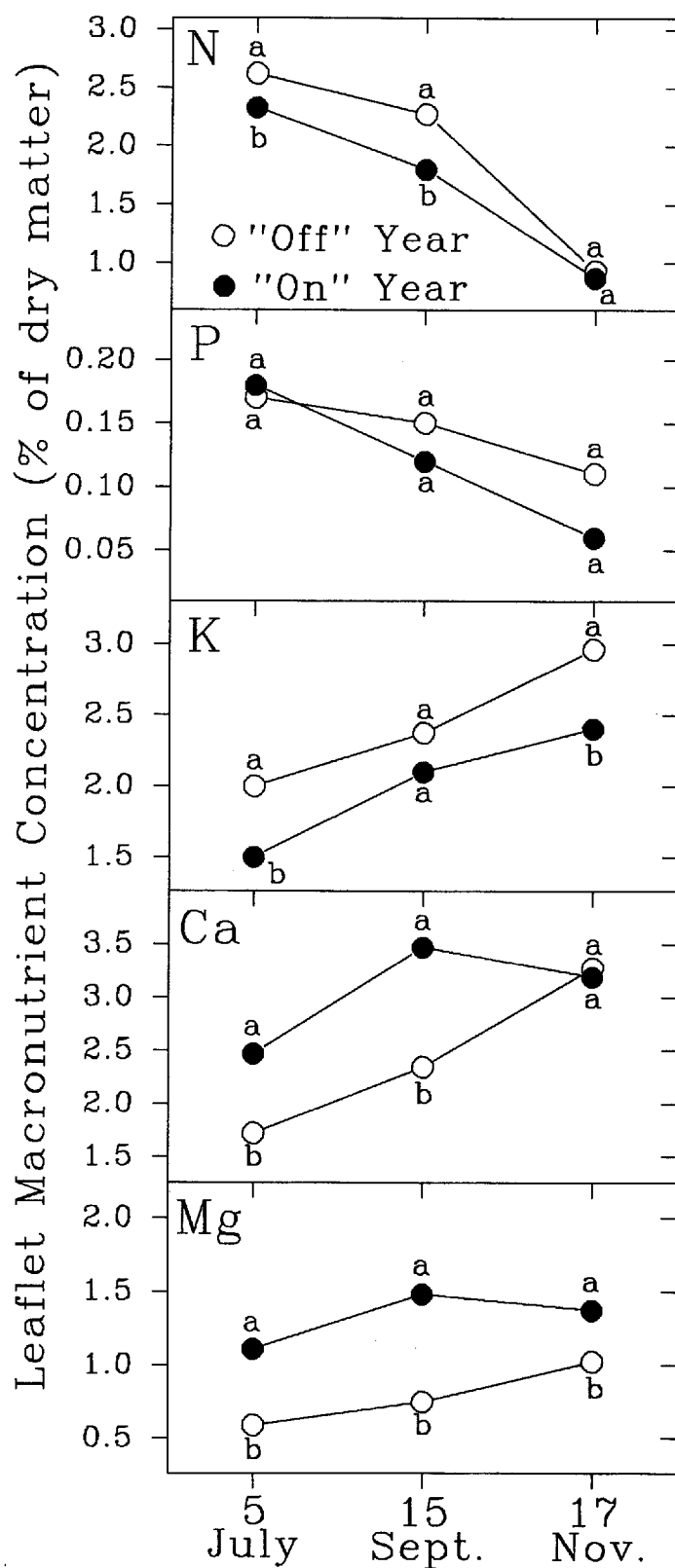


Fig. 1. Leaf macronutrient concentration (percent of dry matter; N, P, K, Ca, and Mg) in alternate-bearing 'Kerman' pistachio trees at the onset of seed fill (5 July), fruit and embryo maturity (15 Sept.), and leaf abscission (17 Nov.). Data are from 1988 and are representative of all years (1988–90); each value is the mean of three tree replications. Mean separation within dates by F test ($P \leq 0.05$).

harvested dry weight but contained >85% of the nutrient in the crop. Thus, only marketable fruit dry weight yield per tree and nutrient contents (from seasonal branch samplings) were considered in this study.

Total dry weight of marketable fruit per tree was determined based on the total fresh weight yield per tree (obtained at fruit maturity), the dry weight to fresh weight ratio of marketable fruit in the mature fruit subsample, and the percentage of marketable fruit in the mature fruit subsample. The total number of marketable fruit per tree was estimated by dividing the total dry weight of marketable fruit per tree by the average dry weight per marketable fruit obtained during the second branch sampling (at fruit maturity). Marketable fruit number per tree was multiplied by the dry weight of individual fruit components (obtained from each branch sampling) to estimate the total embryo and pericarp dry matter accumulation per tree during the spring growth flush (budbreak to the beginning of seed fill) and during seed fill. Because the entire pericarp had to be analyzed at the time of the first branch sampling, the entire pericarp (endocarp and mesocarp/exocarp) was also analyzed at fruit maturity to determine pericarp dry matter and nutrient accumulation during seed fill.

NUTRIENT ANALYSES. Total nutrient contents per tree in leaflets and fruit were estimated to be the product of nutrient concentration expressed as percent dry matter (obtained from five branch samples per tree) and the estimated total canopy dry weight of the corresponding tissue at the time of sampling. Dried tissues were prepared for nutrient analyses as follows: leaflets and combined mesocarp-exocarp (from mature fruit) were ground to pass a 30-mesh screen; endocarps (at fruit maturity) and the entire pericarps (from immature fruit) were ground by hand into small fragments; immature and mature seeds were homogenized in a coffee grinder.

All tissue were analyzed for N, P, K, Ca, and Mg. Total N concentrations were determined using the extraction and analytical procedures described by Weinbaum and Neumann (1977). For the other elements, ground tissue was ashed overnight in a muffle furnace (500 °C) and dissolved in 1 N HNO₃. Potassium concentrations were measured using a Varian Techtron atomic absorption spectrometer (model 120; Sunnyvale, Calif.). Concentrations of the remaining elements were measured using a plasma emission spectrometer (model 3510; Applied Research Laboratories, Sunland, Calif.).

ESTIMATION OF NET NUTRIENT GAIN OR LOSS IN LEAFLETS AND FRUITS. Net nutrient gain or loss in leaflets and fruit in the entire tree canopy were estimated in off-year and on-year trees over the following intervals: a) the spring growth flush—budbreak (late March) to completion of pericarp enlargement (May to June); b) seed fill—onset of macroscopic embryo development (June) until fruit and seed maturity (late August to early September), and c) leaf senescence—fruit maturity (September) until leaf abscission (November). Nutrient accumulation per tree in fruit (all fruit tissues combined) was estimated for the spring growth flush and seed fill periods. Nutrient accumulation per tree in seeds and pericarps was determined separately during seed fill.

STATISTICAL ANALYSES. During all three seasons (1988–90), we observed identical effects of cropping on leaflet nutrient concentration per unit of dry matter and leaflet nutrient content per unit leaf area. Thus, these data are reported only for 1988, and are the mean of three on-year and three off-year tree replications. Unless noted, seasonal net nutrient accumulation or reduction in leaflets and fruits (on a per tree basis) is presented as the mean of three seasons (1988–90), each season consisting of three on-year and three off-year tree replications. On-year and off-year tree means were separated by F tests using the one-way analysis of variance

for a completely randomized design on MSTAT-C, version 2.11 (Michigan State Univ., East Lansing).

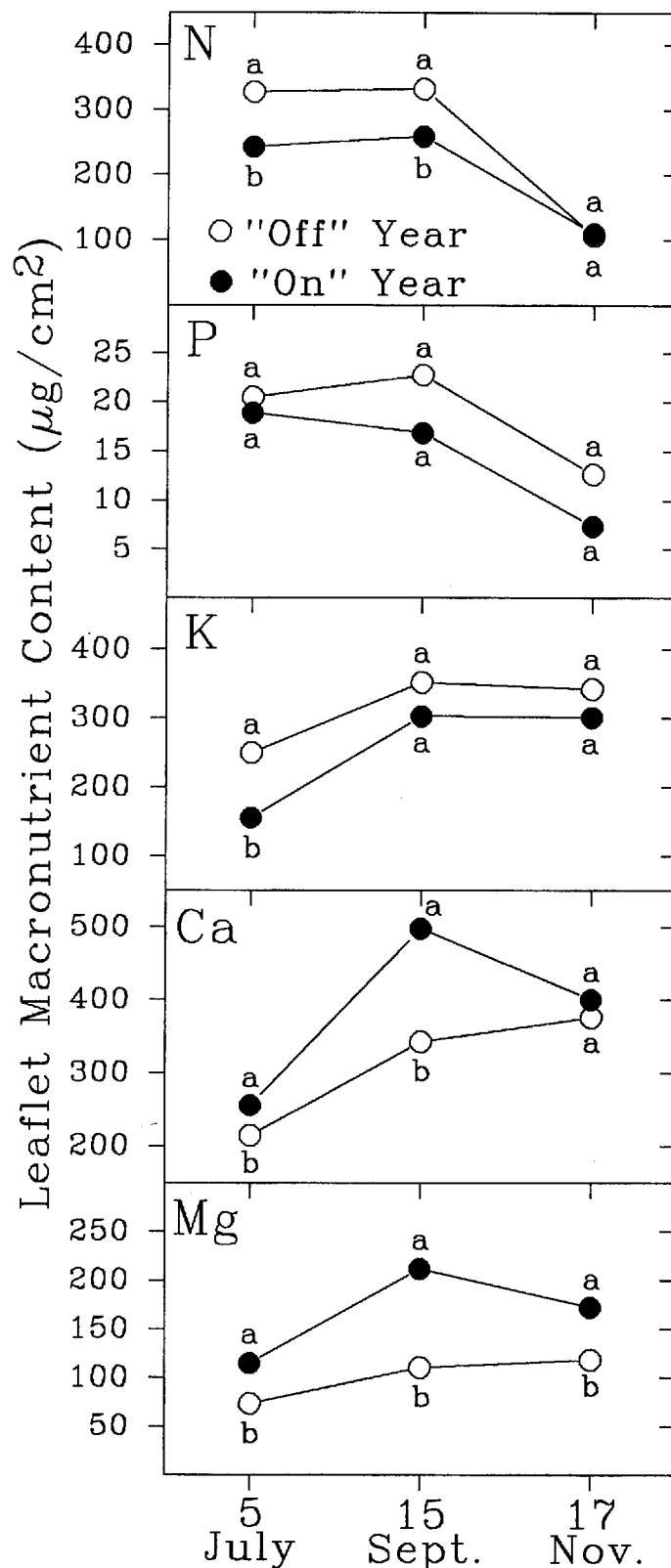


Fig. 2. Leaf macronutrient content (per unit of leaflet area; N, P, K, Ca, and Mg) in alternate-bearing 'Kerman' pistachio trees at the onset of seed fill (5 July), fruit and embryo maturity (15 Sept.), and leaf abscission (17 Nov.). Data are from 1988 and are representative of all years (1988–90); each value is the mean of three tree replications. Mean separation within dates by F test ($P \leq 0.05$).

Table 1. Influence of cropping on net change in leaf macronutrient concentration.^z

Species		Nutrient					Reference
		N	P	K	Ca	Mg	
Almond ^y	[<i>Prunus dulcis</i> (Mill.) Webb.]	NC	NC	NC	NC	ND	Weinbaum and Muraoka, unpublished
Apple	(<i>Malus domestica</i> Borkh.)	+	CD	–	+	+	Bould, 1966
Citrus	(<i>Citrus reticulata</i> Blanco)	–	–	–	+	+	Golomb and Goldschmidt, 1987
Kiwifruit ^y	[<i>Actinidia deliciosa</i> (A. Chev) C.F. Liang et A.R. Ferguson]	NC	NC	–	+	NC	Smith et al., 1987
Peach	[<i>Prunus persica</i> (L.) Batsch]	+	NC	–	+	+	McClung and Lott, 1956
Pecan	[<i>Carya illinoensis</i> (Wangenh.) C. Koch]	–	NC	–	+	+	Diver et al., 1984
Pistachio ^x	(<i>Pistacia vera</i> L.)	–	NC	+	+	+	Current study
Prune	(<i>Prunus domestica</i> L.)	+	ND	–	+	+	Weinbaum et al., 1994c

^zChanges expressed as a percentage of leaf dry weight; + (increase); – (decrease); ND (no data presented); NC (no significant change); CD (conflicting data).

^yData based on cropping and noncropping limbs on the same trees/vines.

^xData based on current study.

Results and Discussion

LEAFLET NUTRIENT CONCENTRATION AND CONTENT PER UNIT LEAF AREA. Leaflet N concentrations were greater in off-year than on-year trees following the spring flush of growth (5 July) and seed fill (15 Sept.; Fig. 1). At the time of leaf abscission (17 Nov.), however, these differences were no longer apparent. When data are expressed as leaf N content (N per unit leaf area), there appeared to be minimal change during seed fill (Fig. 2). The apparent contradiction between data expressed as concentration (Fig. 1) and content (Fig. 2) is easily reconciled if we appreciate that data expressed as a nutrient concentration (percent dry matter) may be influenced by changes in leaf dry weight and leaf nutrient content. Apparent seasonal decreases in leaf nutrient concentrations may be due to seasonal increases in leaf mass (Marini and Marini, 1983;

Oland, 1963) rather than actual decreases in leaf nutrient content (Rogers et al., 1953). Conversely, increases in leaf nutrient concentration over the season indicate that a) nutrient accumulates as the season progresses and b) the rate of nutrient accumulation exceeds the rate of dry matter accumulation in leaves. In general, leaf N and P concentrations decreased over the season, whereas leaf K, Ca, and Mg concentrations increased during seed fill, and K concentration increased until the time of leaf abscission (Fig. 1). The 40% increase in leaf K concentration during the period of seed fill (calculated from the on-year data in Fig. 1) is atypical of other tree fruit species (Table 1) and is associated with the greater apparent K uptake during an “on” year (Brown et al., 1995).

Leaf N and P contents (Fig. 2) remained relatively stable during seed fill and then declined during leaf senescence as these phloem-mobile nutrients are resorbed before leaf abscission. Nitrogen

Table 2. Temporal patterns of net macronutrient accumulation (g/tree) by fruit and leaves in alternate-bearing (AB) ‘Kerman’ pistachio trees during spring flush, seed fill, and leaf senescence (1988–90). Spring flush refers to the period between budbreak and macroscopic embryo enlargement, seed fill refers to the period between the onset of macroscopic embryo enlargement and fruit maturity, and leaf senescence refers to the period between fruit maturity and leaf abscission.^z

Element	AB phase	Annual macronutrient accumulation (g/tree)							Nutrient allocation during leaf senescence (g/tree)	
		Spring flush			Seed fill			Annual total	To orchard	
		Fruit	Leaves	Total	Fruit	Leaves	Total		floor in leaf litter	Resorbed nutrients ^y
N	Off	---	495	495	---	60	60	555	167	–388
	On	395	267	661	354	38	392	1054	134	–171
			**	NS		NS	*	*	NS	**
P	Off	---	33	33	---	6	6	39	23	–12
	On	46	21	67	62	1	63	130	9	–9
			*	*		NS	**	*	NS	NS
K	Off	---	402	402	---	191	191	593	555	0
	On	198	157	354	287	178	465	820	314	8
			***	NS		NS	*	NS	NS	NS
Ca	Off	---	314	314	---	209	209	523	557	59
	On	27	257	284	34	263	297	581	424	–80
			*	NS		NS	*	NS	NS	*
Mg	Off	---	109	109	---	56	56	165	169	11
	On	23	123	146	27	101	128	274	174	–40
			NS	*		**	**	*	NS	**

^zEach value is the mean of three yearly replications, each involving three off-year and three on-year trees (1988 and 1989 only for P, K, Ca, and Mg leaf senescence).

^yNegative values indicate net leaf nutrient resorption (loss) and presumably represent significant fractions of the nutrient pool stored overwinter in perennial tree organs. Positive values indicate net leaf nutrient accumulation.

NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

content per unit leaf area was greater in off-year than on-year trees at the end of both the spring growth flush (5 July) and seed fill (15 Sept.). In contrast to N and P, K, Ca, and Mg content per unit leaf area increased during seed fill (Fig. 2). Calcium and Mg contents per unit leaf area were greater in on-year than off-year trees at the end of the spring growth flush, following seed fill, and following leaf abscission (Mg only).

NUTRIENT ACCUMULATION PER TREE IN LEAVES AND FRUIT. During 1988–90, the estimated leaflet dry weight per tree, leaflet area per tree (both determined in August), and the leaflet number per tree (determined in July) averaged 44%, 43%, and 20% greater, respectively, in off-year trees than in on-year trees, as reported earlier (Weinbaum et al., 1994b). Total yields during “on” years (dry weight of marketable and unmarketable fruit) averaged 44, 27, and 58 kg per tree in 1988, 1989, and 1990, respectively ($cv = 36\%$).

By the end of the spring flush period, the accumulation of N, P, and K in leaflets averaged 1.9, 1.6, and 2.6 times greater, respectively, in off-year than in on-year trees (Table 2). These whole-canopy differences resulted from the combined influences of greater nutrient content per unit leaf area (N and K in Fig. 2) and the greater amount of foliage per tree in the “off” year (Weinbaum et al., 1994b). Leaf macronutrient accumulation did not vary significantly between off-year and on-year trees during the seed fill period, except for Mg (Table 2). As a result of the prior completion of leaf expansion (April to May), leaf accumulation of N and P was relatively insignificant during seed fill.

In the following discussion, total (net) nutrient accumulation refers to the quantities of macronutrients (N, P, K, Ca, and Mg measured in this study), which accumulated per tree in annual, above-ground organs (leaflets plus fruit in on-year trees; leaflets only in off-year trees). Nitrogen accumulation during the spring flush varied annually with crop load in on-year trees. In the relatively low crop year (1989), the leaf N accumulation by off-year trees averaged 35 g greater than the combined N accumulation in leaves and fruit of on-year trees during the spring flush (data not presented). On average, however, N accumulation in leaves and fruit of on-year trees was 167 g more than leaf N accumulation by off-year trees during the spring flush, although this difference was not statistically significant (Table 2 is a 3-year, 1988–90 average).

As shoot elongation and leaf expansion are completed within the spring flush period, macronutrient accumulation in above-ground annual organs in off-year trees occurred primarily between April and June (Table 2). Even in “on” years, 53% of fruit N, 43% of fruit P, and 41% of fruit K accumulation occurred before seed fill. In addition, 44% to 46% of fruit Ca and Mg accumulated during the spring flush, but this demand was relatively low on a mass basis. The on-year demand for fruit N and P before seed fill is likely met, in part, by mobilized N and P reserves, which are present in greater amounts in perennial organs of dormant pistachio trees just before the start of an “on” year (e.g., following the completion of an “off” year; Brown et al., 1995).

In on-year trees, the nutrient requirements of embryo development (seed fill) increased the magnitude and extended the duration of significant nutrient acquisition by annual organs (Table 2). For example, 47% to 59% of fruit N, P, and K accumulation occurred during the seed fill period. Figure 3 illustrates the patterns of relative macronutrient demand during the spring flush and seed fill periods (percentage values calculated from Table 2). During an “off” year, most of the macronutrient accumulation by leaves (particularly N and P) occurs during spring flush. In an “on” year, the macronutrient demand by leaves plus fruit is more extended throughout the season.

The relative fruit demand for N and P expressed as a percentage

of total demand (leaflets plus fruit) was greater during seed fill than during the spring flush of growth (Table 3). This reflects changing

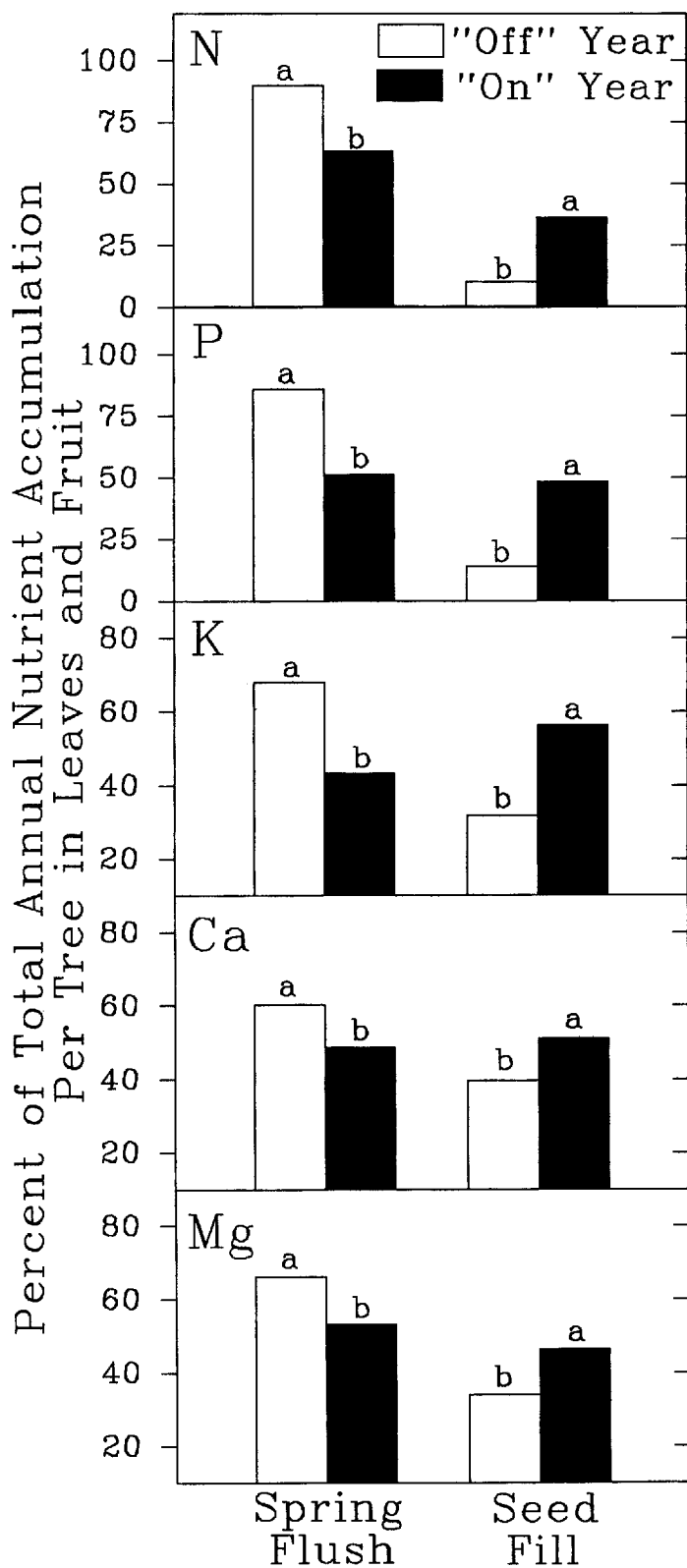


Fig. 3. Net macronutrient accumulation in leaves and fruit of alternate-bearing ‘Kerman’ pistachio trees during the periods of spring flush and seed fill, expressed as a percentage of the total accumulation over both periods (from Table 2). Bars represent the mean of three yearly replications (1988–90), each involving three off-year and three on-year trees. Mean separation between adjacent bars by F test ($P \leq 0.05$).

Table 3. Relative nutrient accumulation in whole fruit during spring flush and seed fill in on-year 'Kerman' pistachio trees (1988–90). Data expressed as a percentage of the total nutrient accumulation in leaves plus fruit ($[\text{g/tree in fruit} + \text{g/tree in leaves plus fruit}] \times 100$). See Table 2 for definitions of spring flush and seed fill.²

Element	Fruit nutrient accumulation (% of nutrient accumulation in leaves + fruit)	
	Spring flush	Seed fill
N	59 b ^y	90 a
P	68 b	99 a
K	55 a	61 a
Ca	9 a	11 a
Mg	15 a	20 a

²Each value is the mean of three yearly replications, each involving three on-year trees.

^yMean separation across elemental rows by F test ($P \leq 0.05$).

fruit-to-leaflet macronutrient demand patterns and preferential allocation of N and P to the developing seed. In contrast to N and P, the accumulation of K, Ca, and Mg in fruit (relative to the total fruit plus leaflet accumulation) did not change significantly between the spring flush and seed fill periods (Table 3). Throughout their development, fruit accounted for no more than 20% of the total (leaflet plus fruit) accumulation of Ca and Mg. The greater accumulation of Ca and Mg in leaves compared to fruit is consistent with the lack of Ca and Mg mobility relative to N, P, and K as reported in other fruit tree species (Batjer and Westwood, 1958; Oland, 1963; Rogers et al., 1953; Van Goor and Van Lune, 1980).

A net decrease of 52% to 59% in the N and P content of the pericarp occurred annually during seed fill (data not presented). Almond (like pistachio) is a dry drupaceous fruit, and, like pistachio, also exhibited a 50% to 60% reduction in pericarp N content during embryo maturation (Weinbaum and Muraoka, 1986). These data are consistent with the concept that the pericarp may serve as a nutrient reservoir during embryo maturation. If expressed as a percentage of embryo accumulation of N and P during seed fill, the redistribution represents 32% of embryo N accumulation per tree and 26% of total embryo P accumulation per tree (Table 4). Conversely, there was a net increase of K, Ca, and Mg in the pericarp during seed fill equivalent to 154%, 62%, and 35%, respectively, of the amount accumulated by the embryo (Table 4).

LEAF NUTRIENT RESORPTION. At the time of leaf abscission (November), leaf macronutrient quantities per tree (amounts falling to the orchard floor in leaf litter) did not differ significantly between on-year and off-year trees (Table 2). During leaf senescence, net N resorption per tree averaged 217 g greater in off-year than in on-year trees (Table 2). The greater leaf N resorption in off-year vs. on-year trees during the postharvest period is a function of the greater leaf N content at the time of fruit maturation (Fig. 2) and >40% greater leaf area per tree (Weinbaum et al., 1994b). The

difference in N resorption accounts for approximately half of the surplus N contained in perennial organs of dormant trees following the "off" year (Brown et al., 1995), and likely represents a major N source for early season fruit N demand during the ensuing "on" year. Net resorption of P also occurred during leaf senescence (9 to 12 g/tree), but was unaffected by recent cropping history. There was no net K resorption during leaf senescence in either on-year or off-year trees, which contrasts with earlier findings on other fruit tree species (Batjer and Westwood, 1958; Rogers et al., 1953).

Net resorption of Ca and Mg per tree during leaf senescence represented a 15% to 18% reduction in the total leaf Ca and Mg accumulation per tree by the time of fruit maturity (Table 2). These net reductions occurred only following an "on" year. Calcium is thought to be a relatively immobile element in plants (Epstein, 1973; Larcher, 1975; Loneragan et al., 1976), but, in the present study, identical patterns of change (net reduction) in leaf Ca content during leaf senescence occurred with different groups of trees in consecutive "on" years. Accordingly, the greater net export of Ca following an "on" year is associated with significantly greater Ca content in dormant canopy branches (Brown et al., 1995).

Photosynthate and dry matter allocation patterns within trees are controlled predominantly by sink regions (Minchin and Thorpe, 1987; Patrick, 1988, 1991). Among metabolic sinks, fruit and seed appear to dominate C allocation in fruit trees (Cannell, 1985; Heim et al., 1979; Leonard, 1962; Maggs, 1963; Wright, 1989). It appears likely that the allocation of phloem mobile macronutrients (especially N, P, and K) are controlled similarly in monocarpic plants (Hill, 1980; Thorne, 1985), but nutrient distribution patterns and nutrient source-sink relationships in fruit trees have received less attention. The following evidence is consistent with the view that fruits (of fruit tree species) represent important sinks for nutrients: a) a linear relationship exists between dry matter and nutrient accumulation by fruit (Clark and Smith, 1988; Rogers and Batjer, 1954), b) fruit accumulate nutrients irreversibly during growth, c) nutrient concentrations increase in developing fruit relative to leaves (Van Goor and Van Lune, 1980; in the present study, seed to leaflet N and P concentration ratios increased by 15% and 25%, respectively, during seed fill; data not shown), and d) the nutrient content of mature fruit (especially N and K) may represent a high percentage of tree nutrient content in heavily-cropping trees (Golomb and Goldschmidt, 1987; Weinbaum et al., 1994c). In the latter studies, K uptake by the trees was increased in response to the K demand of developing fruit.

With few notable exceptions (e.g., Cannell and Kimeu, 1971), the influence of crop load on nutrient uptake in mature, field-grown trees has received little attention. Crop demand for N or K stimulates tree N and K uptake, and may also be linked to N and K depletion of perennial tree organs and leaves adjacent to developing fruit (Weinbaum et al., 1994c). The coupling of fruit accumulation of phloem mobile macronutrients with net leaf nutrient resorption may signal the root system to increase whole tree uptake

Table 4. Net accumulation or reduction (–) in macronutrient content in embryos and pericarps (g/tree) in on-year 'Kerman' pistachio trees during seed fill (1988–90).²

Fruit Component	N	P	K ^y	Ca ^y	Mg ^y
Embryos	517 ± 100	84 ± 14	112 ± 18	21 ± 3	20 ± 3
Pericarps	–163 ± 18	–22 ± 4	173 ± 48	13 ± 2	7 ± 1
Pericarp loss as a percentage of embryo accumulation	32%	26%	---	---	---

²Each value is the mean ± SE of three yearly replications, each involving three on-year trees.

^yPericarps accumulated 154%, 62%, and 35% of the amount of K, Ca, and Mg, respectively, accumulated by the embryo during seed fill.

of the limiting nutrient (see model proposed by Cooper and Clarkson, 1989). Future studies should assess the relative capacity for N uptake in on-year and off-year pistachio trees during seed fill.

Using labeled N in multi-year studies, we have previously demonstrated N cycling; e.g., the concurrent N influx (via the transpiration stream), and N efflux (via the phloem) through mature almond and walnut leaves (Weinbaum and Muraoka, 1986; Weinbaum et al., 1994a). Leaf N content remained stable during almond fruit maturation (Weinbaum and Muraoka, 1986), indicating similar rates of N influx and efflux. In addition, leaf N concentrations of many fleshy fruit species (e.g., apple, kiwi, peach, and prune) do not decline in heavily cropping trees (Table 1). In contrast, leaf N concentrations decline during seed fill in walnut and pistachio (Table 1 and Fig 1; Weinbaum et al., 1994a), and these species remove 2 to 4 times the N in the crop than pome and stone fruit crops (Weinbaum et al., 1992).

The concentration of a common pool of amino-N cycling throughout the plant may be a key to whole-plant regulation of N uptake (Cooper and Clarkson, 1989; Imsande and Touraine, 1994). According to Cooper and Clarkson (1989), as the demand for N in growth processes (e.g., fruit growth) increases, the level of reduced N in the regulatory, recycling pool decreases, which in turn increases N uptake. Visual (qualitative) evidence is consistent with the concept of demand-driven N uptake in our experimental conditions, since the leaf chlorosis observed within heavily fruiting pistachio branches of unfertilized trees did not occur in adjacent, heavily cropping trees fertilized with N. Accelerated leaf protein degradation (Vessey et al., 1990), transport of phloem mobile amino acids (net leaf N resorption) to pistachio and walnut fruit during seed fill (Weinbaum et al., 1994a), and leaf chlorosis are consistent with the view that fruit represent a large sink for N, and that N uptake from soil during this period is insufficient to meet fruit N demand.

Conclusions

Shoot and leaf development and the lack of significant crop load in off-year pistachio trees combine to make the spring growth flush the principal period of nutrient demand within the above-ground, annual organs. That is, at least 85% of the N and P accumulation in annual organs was concentrated during this relatively brief interval.

In on-year trees, the spring flush of growth encompasses shoot growth, leaf expansion, and pericarp enlargement. This combined demand (for N) was greater in on-year than in off-year trees, although the average, 3-year difference (167 g/tree in Table 2) did not achieve statistical significance ($P \leq 0.05$) with the limited number of individual tree replications. The N demand differential of on-year and off-year trees was widened during the spring flush of the high crop years of 1988 and 1990 (240 to 300 g more N/tree in the "on" year; data not shown), thus the greater the crop, the more likely the on-year tree will truly demand more N at this time.

About 50% of fruit N accumulation occurred during the spring growth flush, but fruit accumulated another 50% during seed fill (late June to July) in on-year trees. Thus, the magnitude of N demand was greater in on-year trees and the duration of need extended throughout the fruit development period (April to August). The reduced leaf N resorption from senescing leaves of on-year tree canopies (Table 2) may condition the need for greater postharvest N uptake in "on" years, but this conclusion must await further experimentation.

If nutrient uptake is conditioned by tree demand for specific nutrients (Weinbaum et al., 1994c), our data suggest that the ferti-

zation requirements may differ between on-year and off-year trees. Based on our estimates, for example, on-year pistachio trees demanded 34% more N than off-year trees during the spring flush of growth, and the 6- to 7-fold greater N demand by on-year trees during seed fill (2 to 3 months later) greatly accentuated this difference. Thus, results of this study provide insight to increasing the efficiency of nutrient use and management in pistachio orchards, not only for determining the magnitude of macronutrient demand for a given year of the alternate-bearing cycle, but also for charting the dynamic patterns of macronutrient demand within a season.

Experimental validation of the magnitude and periodicity of N uptake by mature pistachio trees during the alternate-bearing cycle is needed, however. Our data did not allow determination of the magnitude and temporal pattern of storage N accumulation which may be derived directly from soil N uptake. Presumably, leaf N resorption per tree subsequent to seed fill also contributes to that storage pool.

Literature Cited

- Batjer, L.P. and M.N. Westwood. 1958. Seasonal trend of several nutrient elements in leaves of Elberta peach. *Proc. Amer. Soc. Hort. Sci.* 71:116-126.
- Bould, C. 1966. Leaf analysis of deciduous fruits, p. 651-684. In: N.F. Childers (ed.), *Nutrition of fruit crops*. Horticultural Publications, Rutgers, The State Univ., New Brunswick, N.J.
- Brown, P.H., S.A. Weinbaum, and G.A. Picchioni. 1995. Alternate bearing influences annual nutrient consumption and the total nutrient content of mature pistachio trees. *Trees* 9:158-164.
- Cannell, M.G.R. 1985. Dry matter partitioning in tree crops, p. 160-193. In: M.G.R. Cannell and J.E. Jackson (eds.), *Attributes of trees as crop plants*. Natural Environ. Res. Council; Titus Wilson and Sons, Ltd., Kendal, Cumbria, U.K.
- Cannell, M.G.R. and B.S. Kimeu. 1971. Uptake and distribution of macronutrients in trees of *Coffea arabica* in Kenya as affected by seasonal climatic differences and the presence of fruits. *Ann. Appl. Biol.* 68:213-230.
- Clark, C.J. and G.S. Smith. 1988. Seasonal accumulation of mineral nutrients by kiwifruit. II. Fruit. *New Phytol.* 108:399-409.
- Cooper, H.D. and D.T. Clarkson. 1989. Cycling of amino-nitrogen and other nutrients between shoots and roots in cereals—A possible mechanism integrating shoot and root in the regulation of nutrient uptake. *J. Expt. Bot.* 40:756-762.
- Crane, J.C. and B.T. Iwakiri. 1981. Morphology and reproduction in pistachio. *Hort. Rev.* 3:376-393.
- Diver, S.G., M.W. Smith, and R.W. McNew. 1984. Influence of fruit development on seasonal elemental concentrations and distribution in fruit and leaves of pecan. *Commun. Soil Sci. Plant Anal.* 15:619-637.
- Epstein, E. 1973. Flow in the phloem and the immobility of calcium and boron: A new hypothesis in support of an old one. *Experientia* 29:133-134.
- Golomb, A. and E.E. Goldschmidt. 1987. Mineral nutrient balance and impairment of the nitrate-reducing system in alternate-bearing 'Wilking' mandarin trees. *J. Amer. Soc. Hort. Sci.* 112:397-401.
- Heim, G., J.J. Landsberg, R.L. Watson, and P. Brain. 1979. Ecophysiology of apple trees: Dry matter production and partitioning by young 'Golden Delicious' trees in France and England. *J. Applied Ecol.* 16:179-194.
- Hill, J. 1980. The remobilization of nutrients from leaves. *J. Plant Nutr.* 2:407-444.
- Imsande, J. and B. Touraine. 1994. N demand and the regulation of nitrate uptake. *Plant Physiol.* 105:3-7.
- Jessen, R.J. 1955. Determining the fruit count on a tree by randomized branch sampling. *Biometrics* 11:99-109.
- Johnson, R.S. and S.A. Weinbaum. 1987. Variation in tree size, yield, cropping efficiency, and alternate bearing among 'Kerman' pistachio trees. *J. Amer. Soc. Hort. Sci.* 112:942-945.

- Larcher, W. 1975. Physiological plant ecology, p. 107–113. Springer-Verlag, New York.
- Leonard, E.R. 1962. Interrelation of vegetative and reproductive growth with special reference to indeterminate plants. *Bot. Rev.* 28:253–410.
- Loneragan, J.F., K. Snowball, and A.D. Robson. 1976. Remobilization of nutrients and its significance in plant nutrition, p. 463–469. In: I.F. Wardlaw and J.B. Passioura (eds.). *Transport and transfer processes in plants*. Academic, New York.
- McClung, A.C. and W.L. Lott. 1956. Mineral nutrient composition of peach leaves as affected by leaf age and position and the presence of a fruit crop. *Proc. Amer. Soc. Hort. Sci.* 67:113–120.
- Maggs, D.H. 1963. The reduction in growth of apple trees brought about by fruiting. *J. Hort. Sci.* 38:119–128.
- Marini, R.P. and M.C. Marini. 1983. Seasonal changes in specific leaf weight, net photosynthesis, and chlorophyll content of peach leaves as affected by light penetration and canopy position. *J. Amer. Soc. Hort. Sci.* 108:600–605.
- Millard, P. 1995. Internal cycling of nitrogen in trees. *Acta Hort.* 373:3–14.
- Minchin, P.E.H. and M.R. Thorpe. 1987. Is phloem transport due to a hydrostatic pressure gradient? Supporting evidence from pressure chamber experiments. *Austral. J. Plant Physiol.* 14:397–402.
- Monselise, S.P. and E.E. Goldschmidt. 1982. Alternate bearing in fruit trees. *Hort. Rev.* 4:128–173.
- Niederholzer, F.J.A., R.M. Carlson, K. Uriu, M.H. Willits, and J.P. Pearson. 1991. Seasonal partitioning of leaf and fruit potassium and fruit dry matter in French prune trees at various potassium levels. *J. Amer. Soc. Hort. Sci.* 116:981–986.
- Oland, K. 1959. Nitrogenous reserves of apple trees. *Physiol. Plantarum* 12:594–648.
- Oland, K. 1963. Changes in the content of dry matter and major nutrient elements of apple foliage during senescence and abscission. *Physiol. Plantarum* 16:682–694.
- Patrick, J.W. 1988. Assimilate partitioning in relation to crop productivity. *HortScience* 23:33–40.
- Patrick, J.W. 1991. Control of phloem transport to and short-distance transfer in sink regions: An overview, p. 167–177. In: J.L. Bonnemain, S. Delrot, W.J. Lucas, and J. Dainty (eds.). *Recent advances in phloem transport and assimilate compartmentation*. Oest Edition, Nantes, France.
- Rogers, B.L. and L.P. Batjer. 1954. Seasonal trends of six nutrient elements in the flesh of Winesap and Delicious apple fruits. *Proc. Amer. Soc. Hort. Sci.* 63:67–73.
- Rogers, B.L., L.P. Batjer, and A.H. Thompson. 1953. Seasonal trend of several nutrients in Delicious apple leaves expressed on a percent and unit area basis. *Proc. Amer. Soc. Hort. Sci.* 61:1–5.
- Smith, G.S., C.J. Clark, and H.V. Henderson. 1987. Seasonal accumulation of mineral nutrients by kiwifruit. I. Leaves. *New Phytol.* 106:81–100.
- Sparks, D. 1977. Effects of fruiting on scorch, premature defoliation, and nutrient status of ‘Chickasaw’ pecan leaves. *J. Amer. Soc. Hort. Sci.* 102:699–733.
- Stassen, P.J.C., H.W. Stindt, D.K. Strydom, and J.H. Terblanche. 1981. Seasonal changes in nitrogen fractions of young Kakamas peach trees. *Agroplanta* 13:63–72.
- Taylor, B.K. 1967. Storage and mobilization of nitrogen in fruit trees: a review. *J. Austral. Inst. Agr. Sci.* 33:23–29.
- Thorne, J.H. 1985. Phloem unloading of C and N assimilates in developing seeds. *Annu. Rev. Plant Physiol.* 36:317–343.
- Titus, J.S. and S.-M. Kang. 1982. Nitrogen metabolism, translocation, and recycling in apple trees. *Hort. Rev.* 4:204–246.
- Tromp, J. 1983. Nutrient reserves in roots of fruit trees, in particular carbohydrates and nitrogen. *Plant and Soil* 71:401–413.
- Van Goor, B.J. and P. Van Lune. 1980. Redistribution of potassium, boron, iron, magnesium and calcium in apple trees determined by an indirect method. *Physiol. Plantarum* 48:21–26.
- Vessey, J.K., C.D. Raper, Jr., and L.T. Henry. 1990. Cyclic variations in nitrogen uptake rate during reproductive growth. *J. Expt. Bot.* 141:1579–1584.
- Weinbaum, S.A. 1988. Foliar nutrition of fruit trees, p. 81–100. In: P.M. Neumann (ed.). *Plant growth and leaf-applied chemicals*. CRC Press, Boca Raton, Fla.
- Weinbaum, S.A. and T.T. Muraoka. 1986. Nitrogen redistribution from almond foliage and pericarp to the almond embryo. *J. Amer. Soc. Hort. Sci.* 111:224–228.
- Weinbaum, S.A. and P.M. Neumann. 1977. Uptake and metabolism of ¹⁵N-labeled potassium nitrate by French prune (*Prunus domestica* L.) leaves and the effects of two surfactants. *J. Amer. Soc. Hort. Sci.* 102:601–604.
- Weinbaum, S.A., R.S. Johnson, and T.M. DeJong. 1992. Causes and consequences of overfertilization in orchards. *HortTechnology* 2:112–121.
- Weinbaum, S.A., T.T. Muraoka, and R.E. Plant. 1994a. Intracanopy variation in nitrogen cycling through leaves is influenced by irradiance and proximity to developing fruit in mature walnut trees. *Trees* 9:6–11.
- Weinbaum, S.A., G.A. Piccioni, T.T. Muraoka, L. Ferguson, and P.H. Brown. 1994b. Fertilizer nitrogen and boron uptake, storage, and allocation vary during the alternate bearing cycle in pistachio trees. *J. Amer. Soc. Hort. Sci.* 119:24–31.
- Weinbaum, S.A., F.J.A. Niederholzer, S. Ponchner, R.C. Rosecrance, R.M. Carlson, A.C. Whittlesey, and T.T. Muraoka. 1994c. Nutrient uptake by cropping and defruited field-grown ‘French’ prune trees. *J. Amer. Soc. Hort. Sci.* 119:925–930.
- Wright, C.J. 1989. Interactions between vegetative and reproductive growth, p. 15–27. In: C.J. Wright (ed.). *Manipulation of fruiting*. Butterworths Ltd., London.