

Translocation and Distribution of ^{14}C -photosynthates in Bearing and Nonbearing Pistachio Branches¹

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Additional index words. *Pistacia vera*, alternate bearing, abscission

Abstract. Movement of ^{14}C -photosynthates in bearing and nonbearing branches of pistachio (*Pistacia vera* L.) was examined during the period of inflorescence bud abscission. Most of the ^{14}C transported from leaves accumulated in developing nuts. Inflorescence buds on defruited trees accumulated twice as much ^{14}C -photosynthate as those on fruiting trees. Inflorescence buds competed poorly against the developing fruit for photosynthate and this might be responsible for inflorescence bud abscission and resultant alternate bearing.

Alternate bearing in pistachio results from abscission of inflorescence buds during July and August when a heavy crop of nuts is being produced (1). The period of bud abscission coincides with that of dry matter accumulation by the kernel. Competition between buds and developing seeds for photosynthates appeared, therefore, to be responsible for bud abscission. There were small variations in sugar and starch content between bearing and nonbearing branches during the bud drop period (4). In spite of the similarity in carbohydrate levels, a heavy crop of nuts usually depresses inflorescence bud growth during the summer (12) and shoot extension the following year (3). Presence of fruit in other cases has been shown to affect growth and developmental processes (shoot growth, root growth, and accumulation of reserve materials) (8). The effect of developing nuts on translocation and distribution of photosynthates from pistachio leaves is discussed in this paper.

Materials and Methods

Experiments were conducted on bearing 'Kerman' trees growing at the Wolfskill Experiment Orchards, Winters, CA. Young fruit were removed by hand from 5 trees in May while 5 adjacent trees were left intact as controls. A single leaf (5-leaflet), generally at the middle of the shoot (Fig. 1), on each of 4 or more shoots with average current growth in length in each group of trees was exposed to $^{14}\text{CO}_2$ on June 15, July 1 and 18, and August 20, always at 9:00 AM.

$^{14}\text{CO}_2$ (0.5 μCi) administered to a leaf enclosed in a clear plastic bag (Fig. 1) was generated by adding 100 μl of 2 N HCl to a vial containing 50 μl Na_2CO_3 (16.4 mCi/mM). A half hour later, an aqueous solution of $\text{Ba}(\text{OH})_2$ was injected into the plastic bag, which was removed a few minutes later. Some precipitate was noted. Treated branches were removed 72 hr later and divided into the following parts: source leaf, other leaves, fruits, current-season's growth, 1-year-old and 2-year-old wood, and individual inflorescence buds. The various parts were weighed, freeze-dried, and re-weighed after which the larger parts were ground in a Wiley mill to pass a 40-mesh screen and the smaller ones to a fine powder in a Moulinex coffee grinder.

A sample of ca 200 mg was combusted in a combustion apparatus (9, 10) at about 1100°C. The resulting CO_2 was captured in 20 ml of scintillation fluid consisting of toluene:methanol:phenylethylamine (4.3:3.0:2.7 by volume) with 0.5% PPO (2,5-diphenyloxazole) and 0.05% POPOP (2,2'-p-phenylenebis 5-phenyloxazole) and assayed for radioactivity in a Packard-Tricarb Model 3375 Liquid Scintillation Spec-

trometer. The total amount of radioactivity recovered after 72 hr in the entire shoot was determined and a percentage of the total computed for each part.

Results and Discussion

Pistachio trees are deciduous, shoot extension and leaf expansion generally beginning the latter part of March and terminating the end of April. Axillary buds on current shoots (Fig. 1) normally have initiated floral primordia by June 30 after which no further differentiation of floral parts occurs during the summer (12). These buds expand and flower the following April.

Inflorescence buds and ovules began enlarging in early May and mid June, respectively (Fig. 2). The nucellus and integument of the pistachio fruit, unlike other drupes do not undergo extensive growth until 4 or 5 weeks after the endocarp reaches its ultimate size on May 15. The embryo becomes evident about June 15 and its subsequent growth pattern to maturity

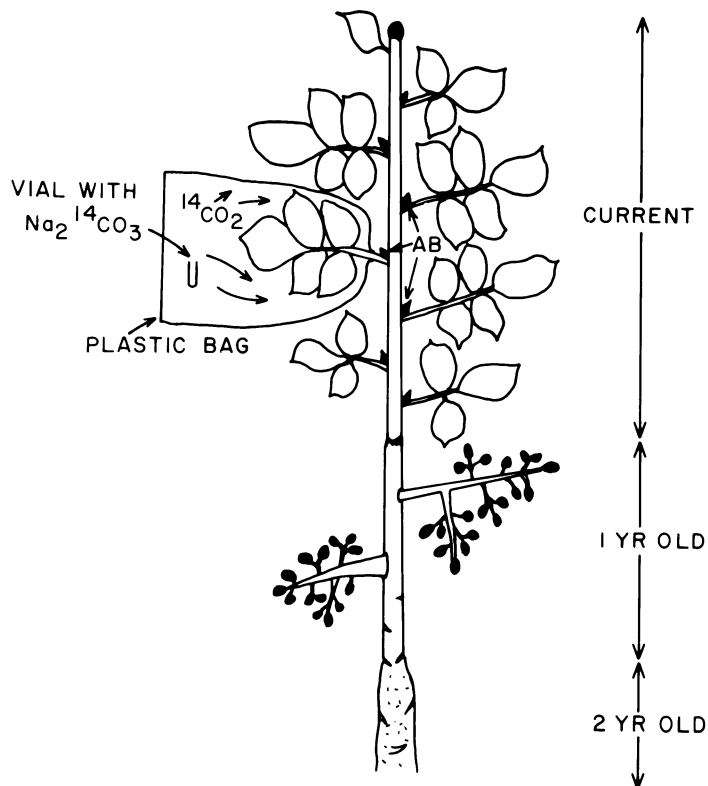


Fig. 1. Schematic representation of a bearing pistachio branch. Axillary inflorescence buds (AB) are subtended by pinnately compound leaves on current-season's growth. Fruit are borne on 1-year-old wood.

¹Received for publication April 1, 1980.

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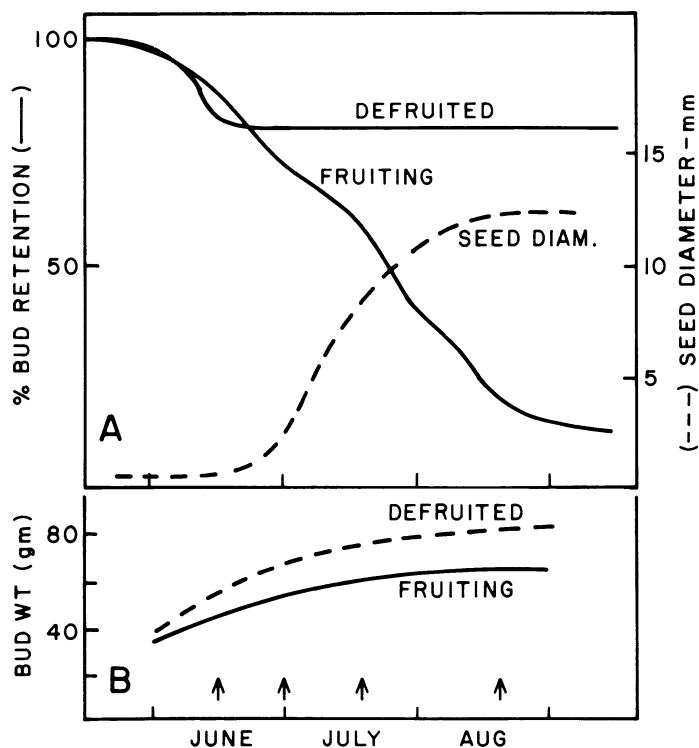


Fig. 2. Curves depicting influence of developing seeds on retention (A) and growth (B) of inflorescence buds. Arrows indicate dates on which ^{14}C was administered to leaves.

is sigmoidal. Inflorescence bud drop on bearing trees began in early June and continued at a nearly constant rate until the end of August (Fig. 2A). Only 20% remained at that time in contrast to nonbearing branches which retained over 80% of their buds.

Radioactivity recovered from the shoots and fruits 3 days after ^{14}C administration ranged from 25 to 58% of the ^{14}C fed to the leaves (Fig. 3). The variability was presumably due to branch location on the tree, leaf angle to the sun and respiratory loss. Presence or absence of fruit had no effect on the amount of ^{14}C taken up by a leaf, but subsequent distribution of ^{14}C -photosynthates was affected. Less than half of the radioactivity remained in the source leaf on a fruiting shoot 3 days after ^{14}C exposure. The majority of the ^{14}C exported from the treated leaf on a bearing branch was found in the fruit, while most of the radioactivity remained in the source leaf on a non-bearing one. Retention of radioactivity in the latter case is attributed to the slower rate of translocation of photosynthates out of the leaf because a strong sink was lacking. Whether the residual ^{14}C in the leaf was of structural or non-structural nature was not determined.

Radioactivity in defruited branches was distributed to vegetative parts and inflorescence buds. Consequently, these parts contained more radioactivity than their counterparts on fruiting branches. Labelled photosynthates were not transported from one leaf to another. Other studies (5, 11) have shown that there is little or no translocation among mature, fully expanded leaves. Occasionally, ^{14}C -photosynthates accumulated in buds some nodes away from the source leaf. The radioactivity was confined in most cases to current-season's growth and 1-year-old wood regardless of the crop load, but low activity was detected in 2-year-old wood of a few branches (data not presented). Probably ^{14}C -photosynthates would have been detected in older wood had the experiments been extended over longer periods.

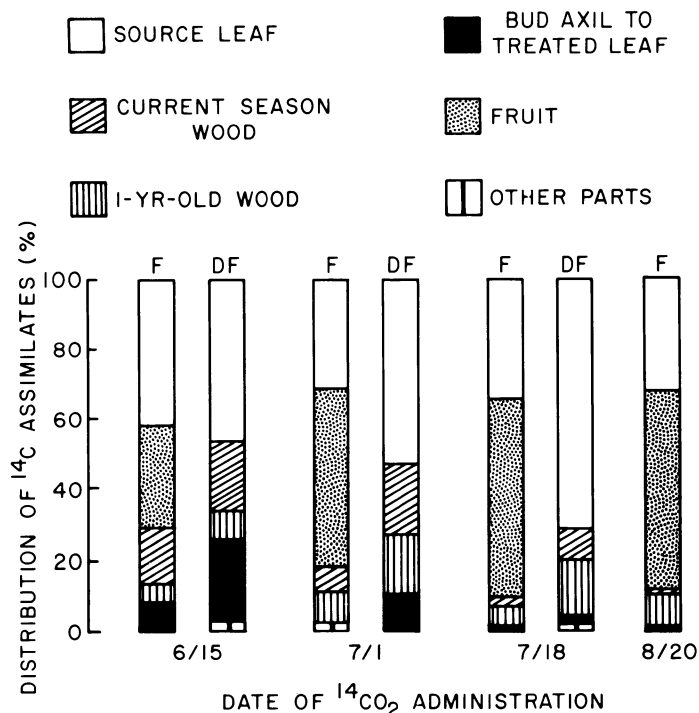


Fig. 3. Mean percentage distribution of recoverable radioactivity from 4 or more pistachio branches 72 hr after exposure to ^{14}C (F = Fruiting; DF = Defruited).

The ^{14}C -photosynthates were translocated bi-directionally in a branch with or without fruit, but the predominate flow was basipetal. Analysis of the current-season's growth which was divided into terminal, middle, and basal sections, revealed that the highest activity was localized in the basal section and the least in the terminal section. Radioactivity translocated into current-season's growth on fruiting and defruited branches decreased from 15.1 and 20.0% on June 15 to 2.7 and 8.0% on July 18, respectively (Fig. 3) and declined to trace amounts in August. Radioactivity in 1-year-old wood during the same period ranged from 16.0 to 5.1% and defruited branches generally accumulated more than those with fruits.

The developing fruit was a strong sink for photosynthates (Fig. 3), the fruit accumulating 29% of the recoverable ^{14}C -photosynthates at the onset of embryo growth and development. Accumulation increased to between 50 and 56% during the period of rapid embryo development. Analysis of dry weight gain showed that seed accumulated dry matter at a nearly

Table 1. Radioactivity in inflorescence buds axillary to treated leaves 3 days after exposure to ^{14}C on different dates.²

Date	Branch	Radioactivity	
		cpm/gm DW	cpm/bud
June 15	DF ^y	1,343,000 ± 376,000	58,500 ± 18,300
	F	785,000 ± 170,000	30,500 ± 3,700
July 1	DF	705,900 ± 333,500	26,000 ± 12,100
	F	301,000 ± 90,000	9,800 ± 3,300
July 18	DF	464,000 ± 99,200	19,800 ± 4,200
	F	248,000 ± 50,800	10,300 ± 3,100

²Each figure is the mean of 4 samples.

^yDF = Defruited; F = Fruiting.

constant rate of 10 mg/day throughout its development (2). The ^{14}C -photosynthates were translocated preferentially to a particular fruit cluster(s) on 1-year-old wood, as individual clusters on the same shoot varied considerably in the amount of radioactivity. Only 1 or 2 clusters, not necessarily the cluster closest to the treated leaf, contained very high activity which suggests that individual clusters depend upon individual leaves for photosynthates. Similar variability was attributed in apples (6) and prunes (7) to vascular connection and phyllotaxy in the shoot. In pecan, the nut closest or on the same side of the shoot to a treated leaf received the highest activity (5).

Inflorescence buds grew rapidly until the end of June, after which growth was slight (Fig. 2B). Buds on defruited trees grew more rapidly and attained 30% more weight than buds on fruiting trees. Cessation of bud growth after June was accompanied by decreasing uptake of ^{14}C -photosynthates. The amount of ^{14}C -photosynthate (cpm/bud) accumulated by the bud in the axil of the source leaf was small compared to that of the fruit (Fig. 3) but the buds had high activity (expressed as cpm/gm dry wt), even greater than that of the fruit. Comparison of the ^{14}C -accumulations by buds on bearing and defruited branches (Table 1) revealed those on nonbearing branches competed more favorably for photosynthates than those on bearing branches. This difference in ability to accumulate photosynthate by the buds was seemingly more than proportional to the growth rates of the buds on nonbearing limbs. However, this difference was not discernible in organogenesis of floral parts within the inflorescence buds (12). Wardlaw (13) states vegetative organs and buds generally receive only photosynthates in excess of those accumulated by fruit.

The earlier conclusion that carbohydrate deficiency appeared not to be responsible for inflorescence bud drop was based on similar sugar and starch levels in bark and wood of bearing and nonbearing branches during the bud-drop period (4). Levels of those components in the buds themselves were not determined. Data obtained in the present study indicate, however, that carbohydrate deficiency may be responsible for the bud drop phenomenon. Inflorescence buds on bearing branches were accumulating about half the ^{14}C -photosynthates

as those on defruited branches when measured June 15 prior to rapid kernel growth and development. This differential translocation pattern continued throughout the sampling period.

Literature Cited

1. Crane, J. C. and M. M. Nelson. 1971. The unusual mechanism of alternate bearing in the pistachio. *HortScience* 6:489-490.
2. _____ and I. M. Al-Shalan. 1974. Physical and chemical changes associated with growth of the pistachio nut. *J. Amer. Soc. Hort. Sci.* 99:87-89.
3. _____ and _____. 1977. Carbohydrate and nitrogen levels in pistachio branches as related to shoot extension and yield. *J. Amer. Soc. Hort. Sci.* 102:396-399.
4. _____, P. B. Catlin, and I. M. Al-Shalan. 1976. Carbohydrate levels in the pistachio as related to alternate bearing. *J. Amer. Soc. Hort. Sci.* 101:371-374.
5. Davis, J. T. and D. Sparks. 1974. Assimilation and translocation patterns of carbon-14 in the shoot of fruiting pecan trees, *Carya illinoensis* Koch. *J. Amer. Soc. Hort. Sci.* 99:468-480.
6. Hansen, P. 1967. ^{14}C -studies on apple tree. 1. The effect of the fruit on the translocation and distribution of photosynthates. *Physiol. Plant.* 20:382-391.
7. _____ and K. Ryugo. 1979. Translocation and metabolism of carbohydrate fraction of ^{14}C -photosynthates in 'French' prune, *Prunus domestica* L. *J. Amer. Soc. Hort. Sci.* 104:622-625.
8. Kozlowski, T. T. and T. Keller. 1966. Food relations of woody plants. *Bot. Rev.* 32:293-382.
9. Peterson, J. I. 1969. A carbon dioxide collection accessory for the rapid combustion apparatus for preparation of biological samples for liquid scintillation analysis. *Anal. Chem.* 31:204-210.
10. _____, F. Wagner, S. Siegel, and W. Nixon. 1969. A system for convenient combustion preparation of tritiated biological samples for scintillation analysis. *Anal. Chem.* 31:189-203.
11. Quinlan, J. D. 1965. The pattern of distribution of 14-carbon in a potted apple rootstock following assimilation of 14-carbon dioxide by a single leaf. *Ann. Rpt. East Malling Res. Sta.* 1964. 117-118.
12. Takeda, F., J. C. Crane, and J. Lin. 1979. Pistillate flower bud development in pistachio. *J. Amer. Soc. Hort. Sci.* 104:229-232.
13. Wardlaw, I. F. 1968. The control and pattern of movement of carbohydrate in plants. *Bot. Rev.* 34:79-105.