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^{14}C-Photosynthate Partitioning in Avocado Trees as Influenced by Shoot Development

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Abstract. **The influence of shoot age on ^{14}C partitioning in potted avocado *(Persea americana* var. *americana* Mill.) trees was determined. The oldest leaf of actively growing shoots and the youngest leaf of previously matured shoots were exposed to $^{14}CO_2$ 18 and 34 days after budbreak (DABB) of new shoots. At these times, treated leaves had a positive net CO_2 assimilation rate and, therefore, were considered to be net C exporters. Sixteen days after ^{14}C exposure, separate plant tissues were harvested, dried, weighed, and oxidized. The percentage of ^{14}C in each tissue was determined by liquid scintillation spectrometry. Photoassimilates were translocated acropetally and basipetally from all treated leaves. However, at 18 DABB, developing leaves of actively growing shoots seemed to be the strongest sink for C assimilated by the oldest leaf of these shoots, whereas the roots were the strongest sink for C assimilated by the youngest leaf of the previously matured shoots. By 34 DABB, roots were the strongest sink for C assimilated by leaves of new and previously matured shoots. These data are useful in developing improved management strategies for controlling phytophthora root rot (incited by *Phytophthora cinnamomi* Rands) in avocados by systemic phosphonate fungicides translocated in the photoassimilate pathway. Thus, phosphonates should be applied after shoots have matured and most of the canopy is in a quiescent state for maximum translocation to the roots.**

A major consideration in the management of avocado orchards in most avocado-producing countries is phytophthora root rot caused by *Phytophthora cinnamomi* (Darvas and Bezuidenhout, 1987; Zentmyer, 1971). This disease is controlled effectively by foliar sprays or trunk injections of systemic phosphonate fungicides (Darvas et al., 1984; Pegg et al., 1985), which are transported acropetally in the xylem and basipetally along with photoassimilates in the phloem (Guest and Grant, 1991). To be effective, these fungicides must be moved basipetally from the leaves to the roots in sufficient concentrations to suppress disease development.

Architecturally, the avocado is defined as a polyaxial species with a usually synchronous growth pattern characterized by alternating shoot and root growth (Verheij, 1986; Whiley et al., 1988). The movement of systemic fungicides in the tree is related to the dynamics of photoassimilate partitioning (unpublished data), which varies with the activity of competing sinks, often temporally separated. The relationship between vegetative flushing and photoassimilate partitioning in the tree indicates the stage of vegetative growth at which systemic fungicides are likely to be transported most effectively to the roots. The objective of this study was to determine the influence of shoot development on photoassimilate partitioning in avocado trees.

Two-year-old 'Simmonds' avocado trees, grafted on 'Waldin' seedling rootstock, were planted in a peat–perlite potting medium (Premix; Premier Brands, Stamford, Corm.) in 12-liter plastic pots. Plants were fertilized at 14-day intervals with an 8N–3P–9K granular fertilizer (Atlantic–Florida East Coast Fertilizer and Chemical Co., Homestead, Fla.) and a 7N–56P–14K soluble fertilizer with minor elements (SOL-U-GRO; Miller Chemical and Fertilizer Corp., Hanover, Pa.) in the irrigation water. Trees were trained to a single leader and, to synchronize growth, were topped at ≈ 15 to 20 cm above the graft union, leaving 10 to 15 mature leaves per tree, and placed in an air-conditioned glasshouse in May 1989. The glasshouse was maintained at 30 ± 2C (day), and 20 ± 2C (night). The axillary bud in the terminal position on each tree was allowed to develop into a new shoot; all other axillary buds were removed (Fig. 1).

Eighteen days after budbreak (DABB) of the new shoot, the oldest leaf on this shoot and the youngest leaf of the previously matured shoot were exposed to $^{14}CO_2$ (Fig. 1). Sixteen days later (34 DABB), when all of the leaves of the actively growing shoot were fully expanded, the oldest leaf on this shoot and the youngest leaf of the previously matured shoot on a different set of trees were exposed to $^{14}CO_2$. Thus, there were two treatments based on the position of the leaf exposed to $^{14}CO_2$: the oldest leaf of the new shoot (T-1) and the youngest leaf of the previously matured shoot (T-2). Each treatment consisted of six single-plant replications at each exposure time in a completely randomized design.

T-1 leaf areas were measured in situ with a leaf area meter (model LI-3000; LI-COR, Lincoln, Neb.) at the time of exposure and at shoot maturity to ascertain their stage of physiological maturity. In addition, net CO_2 assimilation was determined for T-1 and T-2 leaves immediately before treatment to ensure that leaves to be exposed were primarily net C exporters. Net CO_2 assimilation was determined with a portable infrared gas analyzer (Analytical Development Corp., Haddesdon-Herts, England) at a photosynthetic photon flux (PPF) >600 $\mu mol \cdot m^{-2} \cdot s^{-1}$, which is above the light saturation level for avocado (Scholefield et al., 1980).

Trees were labeled with ^{14}C by exposing leaves to $^{14}CO_2$ in a sealed transparent plastic chamber attached to a CO_2 generator, as described by Schaffer et al. (1985). The $^{14}CO_2$ was produced by adding 1 N HC1 to 1 ml of $NaH^{14}CO_3$ (18.5×10^{10} Bq·ml^{-1}) in an Erlenmeyer flask. The gas was circulated continuously through the leaf chamber for 10 min at a flow rate of 2 liters·min^{-1} by a pump attached to the flask and chamber with plastic tubing. Excess $^{14}CO_2$ was absorbed by bubbling the gas through 1 liter of a saturated $Ba(OH)_2$ solution for 3 min to avoid contaminating the environment with $^{14}CO_2$ and prevent nontreated leaves from being exposed to residual $^{14}CO_2$ once the leaf chamber was removed. At the time of $^{14}CO_2$ exposure, PPF in the glasshouse

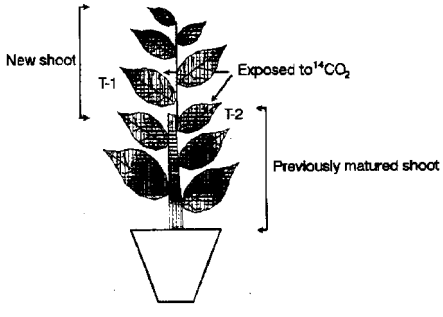

Fig. 1. Schematic diagram of a potted avocado tree illustrating the various shoots and relative positions of leaves exposed to $^{14}CO_2$.

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was >600 µmol·m^{-2}·s^{-1}. Sixteen days after leaves were exposed to $^{14}CO_2$, trees were harvested, organs were separated and oven-dried at 65C, and their dry weights were determined. Material from each organ was ground finely in a spice mill (Black and Decker, Shelton, Corm.), a measured amount of tissue was oxidized in a sample oxidizer (model 306; Packard Instruments, Downersville, Ill.), and ^{14}C from each sample was placed in 20 ml of 1 Carbosorb II :2 Permaflor 5 (v/v) (Packard Instruments), Scintillation fluid (10 ml) was added to the samples for counting. The radioactivity of each sample was determined by radioassay with a liquid scintillation spectrometer (model 5801; Beckman Instrument Co., Fullerton, Calif.). Five nonradio-labeled samples of each tissue also were prepared and assayed for use as standards. The percentage of ^{14}C in each organ was calculated from disintegrations per minute multiplied by organ dry weight and is reported as percentage of total recovered ^{14}C in the plant.

At 18 DABB, the $^{14}CO_2$-exposed T-2 leaf was fully expanded, whereas the $^{14}CO_2$-exposed T-1 leaf was 88% expanded. Leaf area measurement of T-1 at 34 DABB indicated that all leaves of the new shoot were fully expanded, thus the new shoot was mature.

The mean net CO_2 assimilation rates of T-1 and T-2 leaves were 6.1 and 9.2 µmol·m^{-1}·s^{-1}, respectively, at 18 DABB, as determined with the infrared gas analyzer. The lower assimilation rate for T-1 probably was related to the fact that these leaves had not attained maximum photosynthetic capacity, which is reached after full expansion (Schaffer et al., 1991).

More ^{14}C remained in exposed T-1 than T-2 leaves at 18 and 34 DABB (Fig. 2). This result most likely was due to the photoassimilate requirement for leaf expansion and dry-matter accumulation in the younger leaf. Although Schaffer et al. (1991) observed that avocado leaves reach full expansion in ≈ 28 days, dry-matter accumulation continues to increase beyond this point. There was no difference between treatments in ^{14}C partitioning to the stem of the new and mature shoots and to the leaves of mature shoots at either treatment time. At 18-DABB, T-1 accumulated a higher proportion of absorbed ^{14}C in the leaves of the new shoot than T-2 (Fig. 2a). This result indicates that more of the assimilates for current shoot growth were provided by the oldest leaf of the same shoot than leaves of the previously matured shoot. At 18 and 34 DABB, more ^{14}C photoassimilates were partitioned to the roots from the T-2 than the T-1 treatment (Fig. 2), a result that is consistent with ^{14}C translocation patterns in orange *[Citrus sinensis* (L.) Osb.] (Kriedemann, 1969b). However, the difference in assimilate partitioning to the roots between the T-2 and T-1 treatments was greater at 18 DABB.

When ^{14}C-assimilate transport from the T-1 and T-2 leaves was averaged, the developing leaves of the new shoot were a stronger photoassimilate sink than the roots 18 DABB (Fig. 3). However, by 34 DABB, the roots had become a stronger sink. These results agree with those reported for grape *(Vitis vinifera* L.)

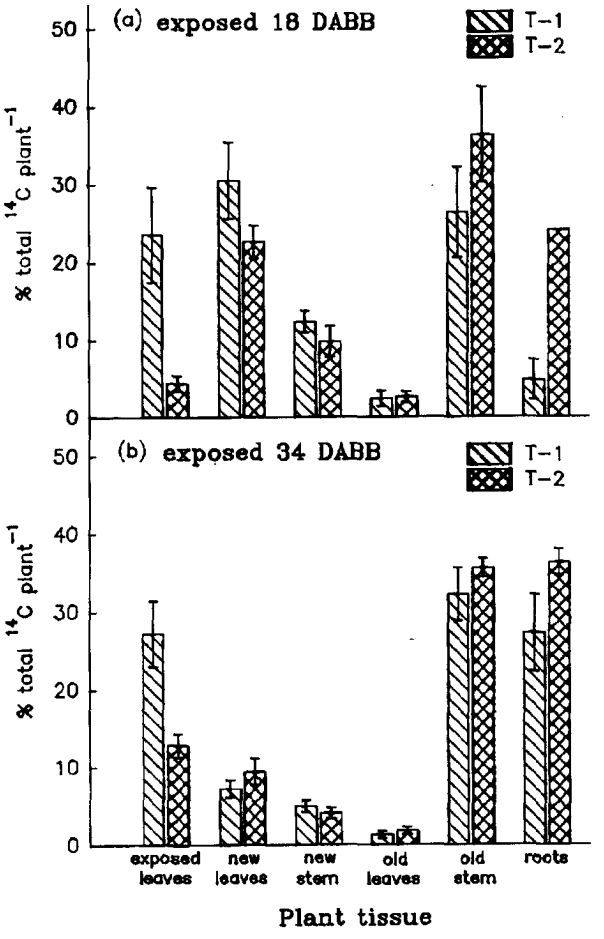

Fig. 2. Partitioning of ^{14}C in avocado trees supplied as $^{14}CO_2$ to the tree (**a**) 18 and (**b**) 34 days after budbreak (DABB) of the newest shoot. Various tissues were analyzed 16 days after exposure to $^{14}CO_2$. T-1 = the oldest leaf of the new shoot that was exposed and T-2 = the youngest leaf of the previously matured shoot that was exposed to $^{14}CO_2$. Exposed leaves = leaves exposed to $^{14}CO_2$, new leaves = all leaves of the new shoot, new stem = stem of the new shoot, old leaves = all leaves of the previously matured shoot, old stem = stem of the previously matured shoot. Vertical lines represent ±SE, where $n = 6$.

(Hale and Weaver, 1962), *Citrus* (Kriedemann, 1969a, 1969b), and pecan *[Carya illinoinensis* (Wangenh.) C. Koch] (Davis and Sparks, 1974), where new shoots were the strongest photoassimilate sink during their growth and development. Spring shoot growth in avocado trees is predominantly from terminal vegetative buds of indeterminate panicles and is synchronized strongly by low winter temperatures, which induce flowering (Davenport, 1982; Venning and Lincoln, 1958; Whiley et al., 1988). This shoot growth occurs at a time

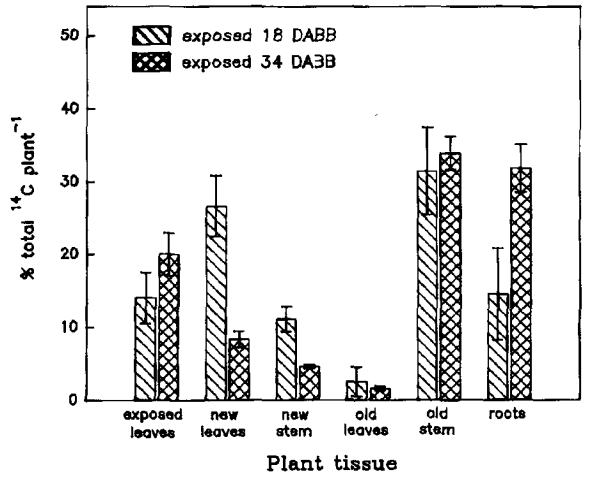

Fig. 3. Partitioning of ^{14}C in avocado trees. Leaves were exposed to $^{14}CO_2$ at 18 or 34 days after budbreak (DABB) of the new shoot and various tissues were analyzed 16 days later. The percentage of ^{14}C in each tissue was calculated by averaging the percentage translocated from the oldest leaf of the new shoot and youngest leaf of the previously matured shoot at each time. Vertical lines represent ±SE, where n = 6.

when the overwintered canopy is losing its photosynthetic efficiency and is approaching senescence (unpublished data), and rising soil temperatures promote the activity of *P. cinnamomi* (Pegg et al., 1982). Growthflushes during summer are typically asynchronous; portions of the canopy remain quiescent, while other areas are in active growth (Whiley et al., 1988). The results from our research indicate that treating trees with phosphonate in spring likely will be most effective after new shoots are mature and will maximize fungicide translocation to the roots. Timing of phosphonate application in summer is not likely to be as critical, since at any one time large portions of the canopy remain in a quiescent state and leaves on mature shoots favor photoassimilate translocation to the roots. This hypothesis requires substantiation using phosphonate treatments at various stages of canopy development.

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