

## CHAPTER 5

# CARBON PARTITIONING IN CONTAINER-GROWN AVOCADO TREES

### 5.1 <sup>14</sup>C-PHOTOSYNTHATE PARTITIONING IN AVOCADO TREES AS INFLUENCED BY SHOOT DEVELOPMENT<sup>‡</sup>

#### 5.1.1 Introduction

A major consideration in the management of avocado orchards in most avocado-producing countries is Phytophthora root rot, caused by *Phytophthora cinnamomi* ( Zentmyer 1971; Darvas and Bezuidenhout 1987). 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 concentration to suppress disease development.

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

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<sup>‡</sup> Whiley, A.W. and Schaffer, B., 1993. <sup>14</sup>C-Photosynthate partitioning in avocado trees as influenced by shoot development. *HortScience* 28, 850-2. APPENDIX 3

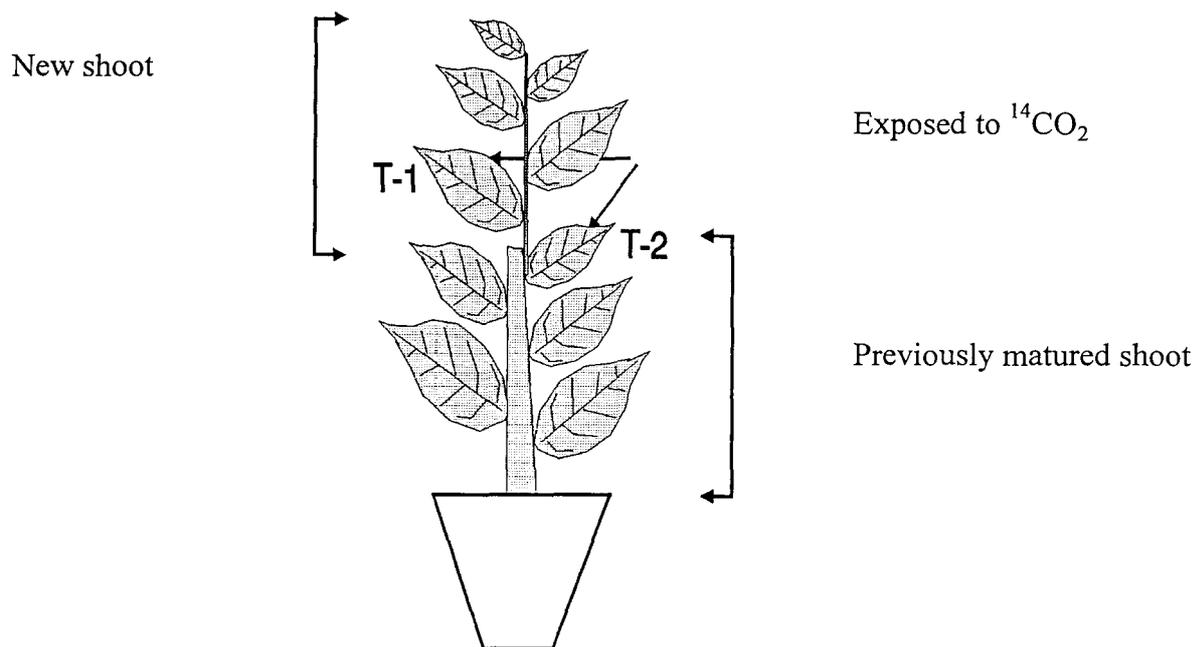
### 5. 1. 2 Materials and Methods

Two-year-old 'Simmonds' avocado trees (a West Indian race cultivar) grafted on 'Waldin' seedling rootstocks, were planted in a peat-perlite potting medium (Promix, Premier Brands, Conn., USA) in 12-l plastic pots. Plants were fertilised at 14-day intervals with a 8N-3P-9K granular fertiliser (Atlantic-Florida East Coast Fertiliser and Chemical Co., Homestead, USA) and a 7N-56P-14K soluble fertiliser with minor elements ((SOL-U-GRO; Miller Chemical and Fertiliser Corp., Hanover, USA) in the irrigation water. Trees were trained to a single leader and, to synchronise growth, were topped at  $\approx 15$  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  $30 \pm 2^\circ\text{C}$  (12 hr day), and  $20 \pm 2^\circ\text{C}$  (12 hr 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. 23).

Eighteen days after bud-break (DABB) of the new shoot, the oldest leaf on this shoot and the youngest leaf of the previously matured shoot were exposed to  $^{14}\text{CO}_2$  (Fig. 23). Sixteen days later (34 DABB), when all 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  $^{14}\text{CO}_2$ . Thus, there were two treatments based on the position of the leaf exposed to  $^{14}\text{CO}_2$ : 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 replicates at each exposure time in a completely randomised design.

T-1 leaf areas were measured *in situ* with a leaf area meter (model LI -3000: LI - COR, Nebraska, USA.) at the time of exposure and at shoot maturity to ascertain their stage of physiological maturity. In addition, net  $\text{CO}_2$  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  $\text{CO}_2$  assimilation was determined with a portable infrared gas analyser (Analytical Development Corp., Haddesdon-Herts, UK) at a photosynthetic photon flux (PPF)  $>600 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ , which is above the light saturation level for avocado (Scholefield *et al.* 1980).

Trees were labelled with  $^{14}\text{C}$  by exposing leaves to  $^{14}\text{CO}_2$  in a sealed transparent plastic chamber attached to a  $\text{CO}_2$  generator, as described by Schaffer *et al.* (1985). The  $^{14}\text{CO}_2$  was



**Fig. 23** Schematic diagram of a containerised avocado tree illustrating the different shoots and relative position of leaves exposed to  $^{14}\text{CO}_2$ .

produced by adding 1 N HCL to 1 ml of  $\text{NaH}^{14}\text{CO}_3$  ( $18.5 \times 10^{10} \text{ Bq ml}^{-1}$ ) in an Erlenmeyer flask. The gas was circulated continuously through the leaf chamber for 10 min at a flow rate of  $2 \text{ l min}^{-1}$  by a pump attached to the flask and chamber with plastic tubing. Excess  $^{14}\text{CO}_2$  was absorbed by bubbling the gas through 1 l of saturated  $\text{Ba}(\text{OH})_2$  solution for 3 min to avoid contaminating the environment with  $^{14}\text{CO}_2$ , and to prevent non-treated leaves from exposure to residual  $^{14}\text{CO}_2$  on removal from the leaf chamber. PPF in the glasshouse was greater than  $600 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  at the time of  $^{14}\text{CO}_2$  exposure.

Sixteen days after leaves were exposed to  $^{14}\text{CO}_2$ , trees were harvested, organs separated and oven-dried at  $65^\circ\text{C}$  and dry mass determined. Material from each organ was finely ground in a spice mill (Black and Decker, Shelton, Conn., USA), a measured amount of tissue was oxidised

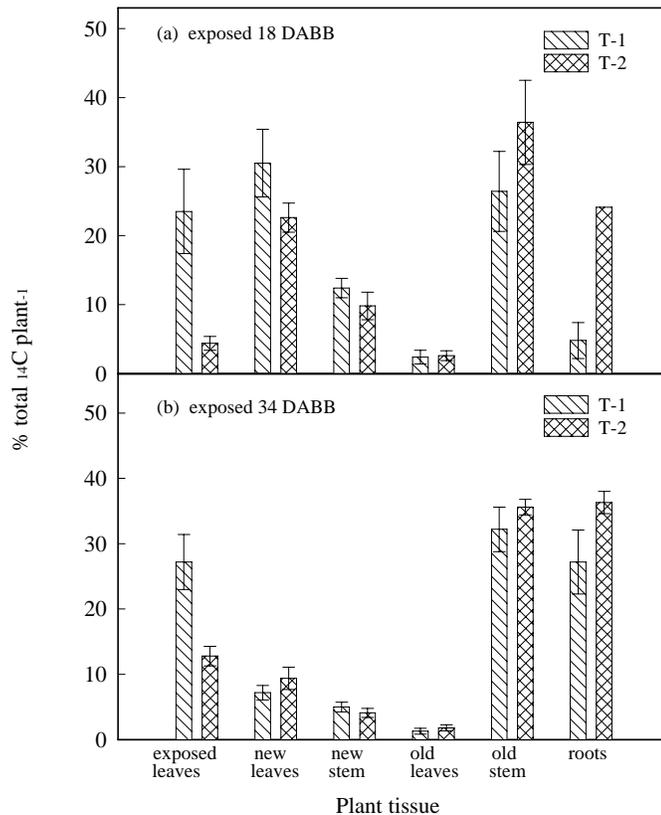
spice mill (Black and Decker, Shelton, Conn., USA), a measured amount of tissue was oxidised in a sample oxidiser (model 306; Packard Instruments, Downersville, USA), and  $^{14}\text{C}$  from each sample placed in 20 ml of 1 Carbosorb II: 2 Permaflor 5 (v:v) (Packard Instruments). Scintillation fluid (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., USA). Five nonradio-labelled samples of each tissue were prepared and assayed for use as standards. The percentage of  $^{14}\text{C}$  in each organ was calculated from the disintegrations per min multiplied by organ dry weight and is reported as the percentage of total recovered  $^{14}\text{C}$  in the plant.

### 5. 1. 3 Results and Discussion

At 18 DABB, the  $^{14}\text{CO}_2$ -exposed T-2 leaf was fully expanded, whereas the  $^{14}\text{CO}_2$ -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 then mature.

The mean net  $\text{CO}_2$  assimilation rates of T-1 and T-2 leaves were 6.1 and 9.2  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , respectively at 18 DABB. The highest rate is lower than those for field-grown trees (Chapter 3), but typical of container-grown trees (Bower *et al.* 1978; Scholefield *et al.* 1980). The lower assimilation rate for T-1 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  $^{14}\text{C}$  remained in the exposed T-1 than T-2 leaves at 18 and 34 DABB (Fig. 24). This most likely was due to 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  $\approx 28$  days, dry matter accumulation continues to increase beyond this point. There was no difference between treatments in  $^{14}\text{C}$  partitioning to the stem of the new and mature shoots and the leaves of the mature shoots at either treatment time. At 18 DABB, T-1 accumulated a higher proportion of absorbed  $^{14}\text{C}$  in the leaves of the new shoot than T-2 (Fig. 24a). This 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  $^{14}\text{C}$  photoassimilates were partitioned to the roots from the T-2 than T-1 treatment (Fig. 24), a result that is consistent with  $^{14}\text{C}$  translocation patterns in orange [*Citrus sinensis* (L.)

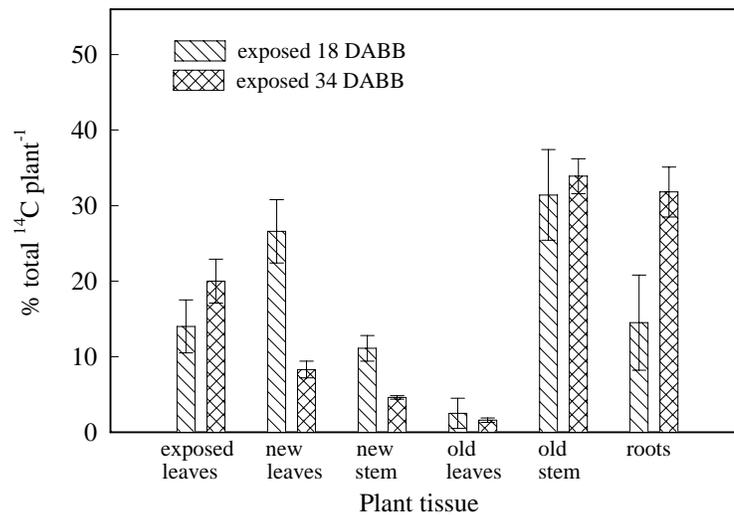
Osby.] (Kriedemann 1969b). However, the difference in assimilate partitioning to the roots between the T-2 and T-1 was greater at 18 DABB.



**Fig. 24** Partitioning of  $^{14}\text{C}$  in avocado trees (a) 18 days and (b) 34 days after bud-break of the newest shoot. T-1 = the oldest leaf of the new shoot, and T-2 = the youngest leaf of the previously matured shoot exposed to  $^{14}\text{CO}_2$ . Exposed leaves = leaves exposed to  $^{14}\text{CO}_2$ , 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  $\pm$  SE where  $n = 6$ .

When  $^{14}\text{C}$ -assimilate transport from 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. 25). However, by 34 DABB the roots had become a stronger sink. These results agree with those reported for grape (*Vitis vinifera* L.) (Hale and Weaver 1962), citrus (Kriedemann 1969a,

1969b), and pecan [*Carya illinoensis* (Wangenh.) K. Koch] (Davis and Sparks 1974) where new shoots in non-fruiting trees were the strongest photoassimilate sink during their growth and development.



**Fig. 25** Partitioning of  $^{14}\text{C}$  in avocado trees. Leaves were exposed to  $^{14}\text{CO}_2$  at 18 or 34 days after bud-break of the new shoot. The percentage of  $^{14}\text{C}$  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  $\pm$  SE where  $n = 6$ .

#### 5. 1. 4 Conclusions

Spring shoot growth in avocado trees is predominantly from terminal vegetative buds of indeterminate inflorescences and is synchronised strongly by low winter temperatures, which induce flowering followed or accompanied by vegetative flushing (Venning and Lincoln 1958; Davenport 1982; Whiley *et al.* 1988a). This shoot growth occurs at a time when the overwintered canopy is losing its photosynthetic efficiency and is approaching senescence (Chapters 2 and 3) and rising soil temperatures promote the activity of *Phytophthora cinnamomi* (Pegg *et al.* 1982). Summer growth flushes typically involve fewer branches;

portions of the canopy remain quiescent, while other branches grow actively (Whiley *et al.* 1988a). The results from this research suggest that spring phosphonate treatment will be most effective after new shoots mature, and will maximise fungicide translocation to the roots which are the target organ for protection. Timing of phosphonate application in summer is not likely to be as critical, since at any one time large portions of the canopy are quiescent and leaves on mature shoots permit more photoassimilate translocation to the roots. This hypothesis requires substantiation using phosphonate treatments at different stages of canopy development, and results from research addressing these areas is reported in Chapter 7.