

## Effect of Fruit Removal on Net Gas Exchange of Avocado Leaves

Bruce Schaffer, L. Ramos, and S.P. Lara

Tropical Research and Education Center, IFAS, University of Florida, 18905 S.W. 280 Street, Homestead, FL 33031

*Additional index words.* *Persea americana*, net photosynthesis, leaf conductance

**Abstract.** All but 10 current-year leaves were removed from girdled branches of avocado (*Persea americana* Mill.) trees having one remaining fruit or all fruit removed. Removing all fruit resulted in increased leaf dry weight per area ( $W_a$ ), a 250% increase in the number of starch grains in leaves, and a reduction in leaf conductance ( $g_1$ ) and net  $\text{CO}_2$  assimilation (A). Internal  $\text{CO}_2$  concentration ( $C_i$ ) was lower for leaves of branches with fruit than for leaves of branches without fruit. The results suggest that the accumulation of starch in defruited, girdled branches results in an inhibition of A. The data suggest that the increased  $g_1$  associated with the presence of avocado fruit is possibly a result of increased A and reduced  $C_i$  levels.

Inhibition of growth or removal of reproductive organs or other sinks for photosynthates decreased net  $\text{CO}_2$  assimilation (A) for many plants (1, 3, 4, 6, 7, 13, 14). Fruit removal results in an accumulation of starch grains in the chloroplast (4, 5, 12). One possible explanation for the effect of fruit removal on reduced A rates is the interference of chloroplast absorption of light or disruption of thylakoid membranes due to starch accumulation in leaves (12).

Several studies have found a decrease in leaf conductance ( $g_1$ ) concomitant with decreased A rates after sink removal (3, 7). Therefore, another proposed explanation for the influence of fruit on A is via a feedback response from the fruit to the leaves controlling the stomatal mechanism (7, 8). The effect of fruit removal on net gas exchange characteristics of avocado has not been reported to the best of our knowledge. The purpose of this study was to test the effect of fruit removal on leaf dry weight per area ( $W_a$ ), A,  $g_1$ , and internal  $\text{CO}_2$  concentration ( $C_i$ ) of avocado leaves.

Eight-year-old 'Booth 7' avocado trees growing at the Tropical Research and Education Center, Univ. of Florida, in southern Florida were used for this experiment. During June 1986, at the time of early fruit development, fruit-bearing branches were girdled at the base and all but 10 current year's leaves per branch were removed. For this cultivar,

anthesis occurred from April to May, and fruit ripened in late summer. Girdled branches were divided into two treatments: a) branches with all fruit removed and b) branches with one fruit allowed to remain. At the time of initial fruit removal, the average fresh weight of the fruit was 30.3 g, which was  $\approx 7\%$  of the fresh weight of a mature fruit of this cultivar. Each treatment consisted of two branches on five separate trees, totaling 10 replications.

Two current-year's leaves of similar ages between treatments were tagged on each branch at the time of initial fruit removal (day 0). Prior to initial fruit removal (day 0) and at 14-day intervals after fruit removal,  $A$ ,  $g_1$ , and  $C_i$  were determined between 9:00 and 11:30 AM from random branches of each treatment.  $W_a$  was determined from two leaves each of 10 additional branches for each treatment. Twenty-eight days after initial fruit removal, all fruit were removed from the branches that had one fruit remaining. Average fresh fruit weight at that time was 90.7 g. Net  $\text{CO}_2$  assimilation,  $g_1$ ,  $C_i$  and  $W_a$  then were determined for leaves of branches of each treatment 14 days later.

Net  $\text{CO}_2$  assimilation,  $g_1$ , and  $C_i$  were determined from  $\text{CO}_2$  and  $\text{H}_2\text{O}$  vapor fluxes in an enclosed leaf chamber connected to a portable gas analyzer (Analytical Development Co., Haddesdon, Herts. U.K.) as previously described (15). The chamber contained a fan (to minimize boundary layer resistance), a humidity sensor, and thermocouples for sensing leaf and air temperatures. Outside air was supplied to the chamber at a flow rate of  $6.25 \text{ ml}\cdot\text{s}^{-1}$  by a mass flow controller. The air stream was first passed through silica gel to absorb some of the moisture and maintain relative humidity in the chamber at  $30\% \pm 1\%$ . Although air temperature in the chamber increased over the measurement period, temperature remained between  $31^\circ$  and  $33^\circ\text{C}$  during determinations. All  $A$ ,  $g_1$ , and  $C_i$  determinations were made well above saturating light levels ( $\text{PPF} > 1600 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ ) as determined by a quantum sensor connected to a LI-1000 data logger (LI-COR). Leaf dry weight per area was determined from the dry weight of five  $0.32\text{-cm}^2$  leaf disks from each of two leaves per branch. Fourteen days after initial fruit removal (day 14), leaf sections were taken from mid-lamina of leaves in each treatment, preserved in formalin-acetic acid-alcohol (FAA), dehydrated in an ethanol-xylene series, and embedded in paraffin. Cross-sections ( $4 \mu\text{m}$ ) were stained with  $\text{I}_2\text{KI}$  and the number and size of starch grains was determined. Starch grains were counted from five random  $767.3\text{-}\mu\text{m}^2$  microscope fields per section at X400.

Prior to initial fruit removal (day 0), there were no differences in  $A$ ,  $g_1$ ,  $C_i$ , and  $W_a$  between treatments (Fig. 1). Fourteen and 28 days after initial fruit removal,  $W_a$  was 25% greater for branches with all fruit removed than branches with one fruit remaining (Fig. 1a).  $C_i$  was slightly higher for branches with all fruit removed than those with one fruit remaining 14 and 28 days after initial fruit removal (Fig. 1d). At these times,  $A$  was 40% to 50% lower and  $g_1$  was 35% to 40% lower for leaves of defruited branches than for leaves of fruiting branches (Fig. 1 b and c). Fourteen days after fruit was removed from all branches (42 days after initial fruit removal), there were no differences in  $A$  or  $g_1$  between treatments (Fig. 1 b and c). At that time,  $W_a$  remained lower for branches that previously had one fruit remaining, although the difference was not as great as during days 14 and 28 (Fig. 1a). Fourteen days after fruit were removed from all branches (42 days after initial fruit removal),  $C_i$  was higher for branches that previously had one fruit remaining (Fig. 1d).

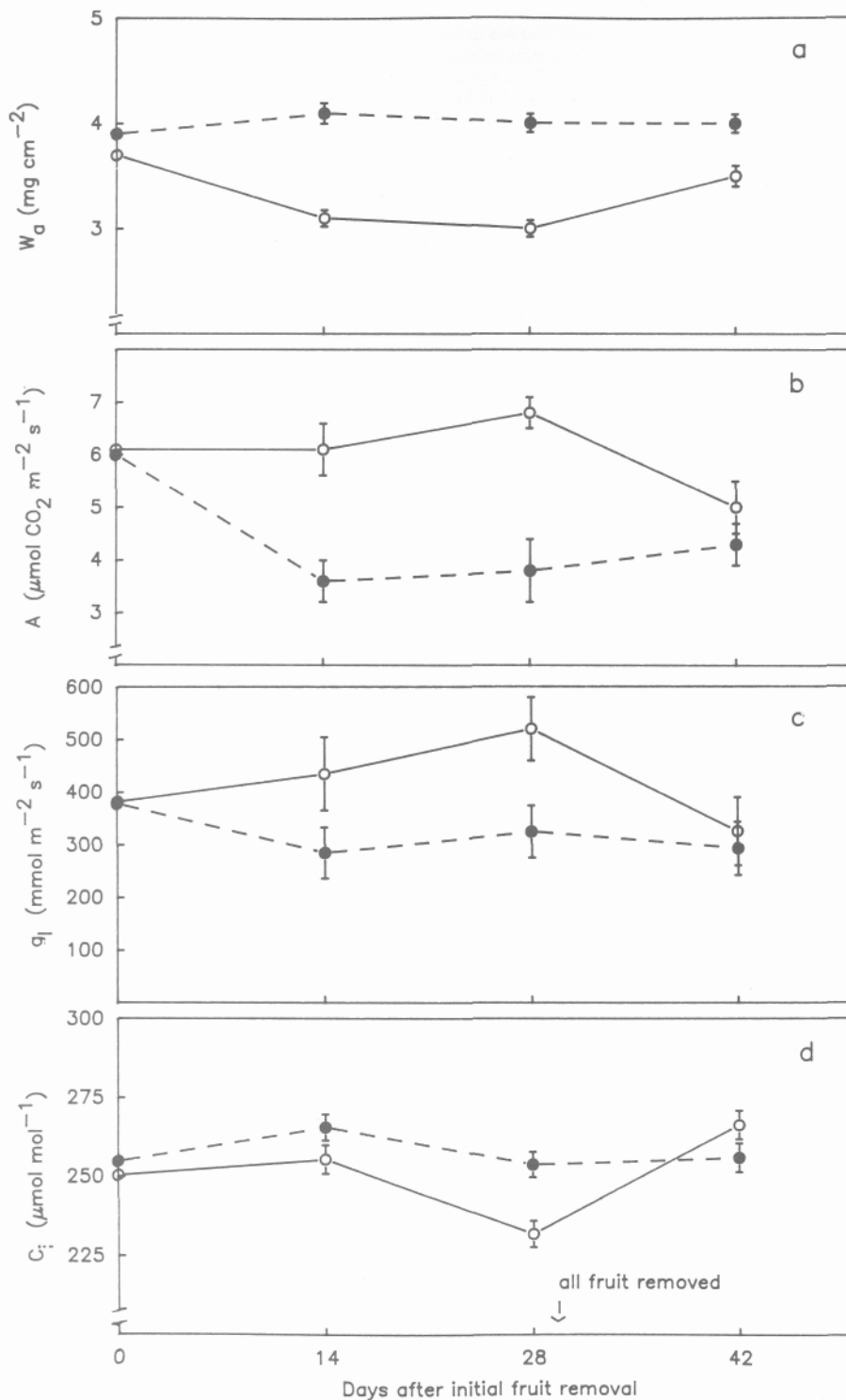


Fig. 1. (a) Leaf dry weight per area ( $W_a$ ), (b) net  $\text{CO}_2$  assimilation (A), (c) leaf conductance ( $g_l$ ), (d) internal  $\text{CO}_2$  concentration ( $C_i$ ) of leaves of avocado branches with (—) and without (- - -) fruit. Data points and vertical bars represent means  $\pm$  1 SE for 20 leaves.

The increase in  $W_a$  after initial fruit removal was presumably due to an increase in carbohydrate accumulation in the leaves in the absence of a fruit sink, since there were no differences in leaf thickness or morphology between treatments. Fourteen days after

initial fruit removal, the average number of starch grains per microscope field was greater for defruited branches than for branches with fruit (27.3 vs. 10.8,  $P = 0.05$ ). Starch grains also appeared larger in leaves of fruiting branches. An increase in nonstructural carbohydrates in the leaves of defruited plants has been observed also for other fruit crops (3, 4, 5, 13, 14). Increased starch concentrations in leaves have been shown to be related to significant reductions in A (9). Therefore, it is likely that the increased starch accumulation in the leaves of deblossomed avocado branches acted as a feedback mechanism resulting in reduced A.

Increased  $g_1$  for fruiting branches was consistent with results found for several species (3, 6, 8, 10). Thus, it has been speculated that the increased A resulting from the presence of a fruit sink is an effect of increased  $g_1$  (3, 7, 8). In a recent review, however, Farquhar and Sharkey (2) concluded that under nonstress conditions,  $g_1$  is rarely limiting to A, and reduced  $g_1$  is often an effect rather than the cause of reduced A. If A is high,  $C_i$  is often reduced due to the rapid fixation of  $CO_2$  (11). This reduction in  $C_i$  can cause stomates to open, resulting in increased  $g_1$ . Thus, if  $g_1$  was limiting to A in defruited plants,  $C_i$  would be expected to change in the same direction as  $g_1$  (2). In the present study, however, the reverse was true. Therefore, although decreased A is associated with decreased  $g_1$  in defruited avocado trees, reduction of  $g_1$  may be an effect rather than the cause of reduced A. Thus, decreased A of leaves of defruited avocado branches was probably due to increased starch granules in the chloroplast, which has been shown in other plants to result in deformation of the chloroplast structure (12). Another consideration is the effect of fruit on the water relations of the leaves that may have resulted in changes in  $g_1$ . Although leaf water potential was not measured during this study, there was ample rain during the experiment and plants showed no apparent signs of water stress. It is more probable that increased A in leaves of fruit-bearing avocado branches was via a carbohydrate-mediated feedback response.

### Literature Cited

1. DeJong, T.M. 1986. Fruit effects on photosynthesis in *Prunus persica*. *Physiol. Plant.* 66:149-153.
2. Farquhar, G.D. and T.D. Sharkey. 1982. Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.* 31:275-278.
3. Forney, C.F. and P.J. Breen. 1985. Dry matter partitioning and assimilation in fruiting and deblossomed strawberry. *J. Amer. Soc. Hort. Sci.* 110:181-185.
4. Hoffmann, E. and F. Lenz. 1974. Die photosyntheseraten und kohlenhydratgehalte der blätter bei fruchttragenden und nicht-fruchttragenden Auberginen und Erdbeerpflanzen. *Gartenbau.* 39:539-547.
5. Hoffmann, E., G. Mix, and F. Lenz. 1975. Der staregehalt der chloroplasten bei fruchttragenden und nicht fruchttragenden Auberginen und Erdbeerpflanzen. *Angew. Bot.* 49:115-121.
6. Lenz, F. and C.N. Williams. 1973. Effect of fruit removal on net assimilation and gaseous diffusive resistance of soybean leaves. *Angew. Bot.* 47:57-63.
7. Mondal, M.H., W.A. Brun, and M.L. Brenner. 1978. Effects of sink removal on

photosynthesis and senescence in leaves of soybean (*Glycine max.* L.) plants. *Plant Physiol.* 61:394-397.

8. Monselise, S.P. and F. Lenz. 1980. Effects of fruit load on stomatal resistance, specific leaf weight, and water content of apple leaves. *Gartenbau.* 45:188-191.
9. Nafziger, E.D. and H.R. Koller. 1976. Influence of leaf starch concentration on CO<sub>2</sub> assimilation in soybean. *Plant Physiol.* 57:560-563.
10. Proctor, J.T.A. 1979. Stomatal conductance changes in leaves of McIntosh apple trees before and after fruit removal. *Can. J. Bot.* 59:50-53.
11. Raschke, K. 1975. Stomatal action. *Annu. Rev. Plant Physiol.* 26:309-402.
12. Schaffer, A.A., K. Liu, E.E. Goldschmidt, C.D. Boyer, and R. Goren. 1986. *Citrus* leaf chlorosis induced by sink removal: starch, nitrogen, and chloroplast ultrastructure. *J. Plant Physiol.* 124:111-121.
13. Schaffer, B., J.A. Barden, and J.M. Williams. 1986. Net photosynthesis, stomatal conductance, specific leaf weight, and chlorophyll content of strawberry plants as influenced by fruiting. *J. Amer. Soc. Hort. Sci.* 111:82-86.
14. Schaffer, B., J.A. Barden, and J.M. Williams. 1986. Whole plant photosynthesis and dry-matter partitioning in fruiting and deblossomed day-neutral strawberry plants. *J. Amer. Soc. Hort. Sci.* 111:430-433.
15. Schaffer, B. and S.K. O'Hair. 1987. Net CO<sub>2</sub> assimilation of taro and cocoyam as affected by shading and leaf age. *Photosynthesis Res.* 11:245-251.