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Effects of leaf age on gas exchange characteristics of avocado (*Persea americana* Mill.)*

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ABSTRACT

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The effect of leaf age on area, dry weight, specific leaf density, chlorophyll concentration, and gas exchange was determined for leaves of avocado (*Persea americana* Mill.). Leaf area and leaf dry weight of cultivars 'Booth-8' and 'Peterson' increased linearly until 28 days after vegetative bud-break and then remained constant. Chlorophyll *a* and total chlorophyll contents increased until 28 and 42 days after bud-break for 'Booth-8' and 'Peterson', respectively. There were no detectable changes in specific leaf density, transpiration (E), or stomatal conductance (g_s) during leaf development and aging. Net CO_2 assimilation (A) increased and dark respiration (Rd) decreased for both cultivars until about 42 days after bud-break and rates then leveled off. The data indicate that avocado leaves function at their physiological optimum from shortly after full leaf expansion until at least 10 weeks after vegetative bud-break.

Keywords: avocado; chlorophyll; gas exchange; photosynthesis; dark respiration; specific leaf density.

Abbreviations: A = net CO_2 assimilation; Rd = dark respiration; PPF = photosynthetic photon flux; E = transpiration; g_s = stomatal conductance for CO_2.

INTRODUCTION

The growth of avocado is characterized by periods of rapid shoot growth separated by relatively quiescent periods (Venning and Lincoln, 1958; Davenport, 1982; Whiley et al,. 1988). The spring flush occurs at the end of anthesis and most of the active terminals produce new leaves. Subsequent apical growth usually occurs during summer and autumn. In moist subtropical cli-

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mates, two to four growth flushes per year may occur on non-fruiting shoots while fruiting shoots may only flush once during the spring. This results in a composite canopy with leaves of varying ages.

The dynamics of the transition of avocado leaves from sink to source and changes in their photosynthetic efficiency as they age have not been established. It has been shown with other plants that as leaves expand, net CO_2 assimilation increases, reaching a peak some time after the leaf reaches full size (Leopold and Kriedemann, 1975). However, there appear to be differences among species in leaf development and the transition of leaves from sink to source (Kriedemann, 1968; Watson and Landsberg, 1979). A key factor determining the success of fruiting is the seasonal photosynthetic efficiency (Cannell, 1985) during critical stages of development. Establishing the effect of leaf age on photosynthetic characteristics of avocado leaves will provide basic information assisting in the management of avocado canopies for maximum photosynthetic efficiency and yield. This note reports on the effects of leaf age on expansion and photosynthetic efficiency of avocado leaves.

MATERIALS AND METHODS

Avocado cultivars 'Booth-8' and 'Peterson' planted at the University of Florida's Tropical Research and Education Center, Homestead, FL (25°S, 3 m above sea level) were used in this experiment. All trees were on cultivar 'Waldin' seedling rootstocks and were 12–14 years old at the beginning of the experiment. Trees were irrigated twice weekly with a rotating water canon providing an average of 38 mm h^{-1} of water. Trees were fertilized according to standard commercial practices (Malo and Campbell, 1983).

Similar-aged leaves were selected for growth and gas exchange determinations on each of five randomly chosen trees for each cultivar immediately after vegetative buds opened (August for 'Peterson' and September for 'Booth-8'). Leaf area, leaf dry weight, and specific leaf density were determined on two randomly selected leaves per tree at 3-day intervals from 7 days after bud-break until leaves were fully expanded (28 days after bud-break). Chlorophyll concentrations were determined for two leaves per tree at 7-day intervals from 14 days after bud-break to 42 days after bud-break. Leaf area was measured with a LiCor Model LI-3000 leaf area meter (LiCor Inc., Lincoln, NE). Leaf dry weight was determined after drying the leaves for 5 days at 70°C. Specific leaf density was calculated from the dry weight of five 0.32 cm^2 leaf disks. For chlorophyll determinations, four disks totaling 1.28 cm^2 were sampled from each side of the midrib of each leaf. Chlorophylls *a* and *b* were extracted from four of these disks as described by Arnon (1949). Gas exchange determinations were made for three leaves (of similar ages as those used for chlorophyll determinations) on newly developing non-fruiting shoots on each tree. The leaves selected for gas exchange determinations were lo-

cated two nodes below the shoot apex. Net CO_2 assimilation (A), stomatal conductance for CO_2 (g_s), transpiration (E), and dark respiration (Rd) were determined for the same leaves at approximately 7-day intervals (depending on weather conditions) from 14 days after bud-break until a severe freeze caused all leaves to abscise (104 days and 139 days after vegetative bud-break for 'Booth-8' and 'Peterson', respectively).

Net CO_2 assimilation, g_s, and E were determined with a portable gas and water vapor exchange analyzer (LCA-2, Analytical Development Co., Hoddesdon, Herts., UK) as described by Schaffer et al. (1987). Outside air containing 340 ± 10 μmol CO_2 mol^{-1} and dried to a constant relative humidity of $25 \pm 5\%$, was pumped into the chamber at 0.4 l min^{-1}. Air temperature in the chamber was 33 ± 2°C. All gas exchange determinations were made between 10 and 16 h at a photosynthetic photon flux (PPF) above 600 μmol m^{-2} s^{-1}, which is above the light saturation point for avocado (Scholefield et al., 1980). Dark respiration was determined as described for A, except that the leaf chamber was enclosed in two layers of black plastic to exclude light during the measurements. Measurements were recorded 10 min after leaves were enclosed in the chamber. Air temperatures and relative humidity in the chamber were similar to those described for A determinations.

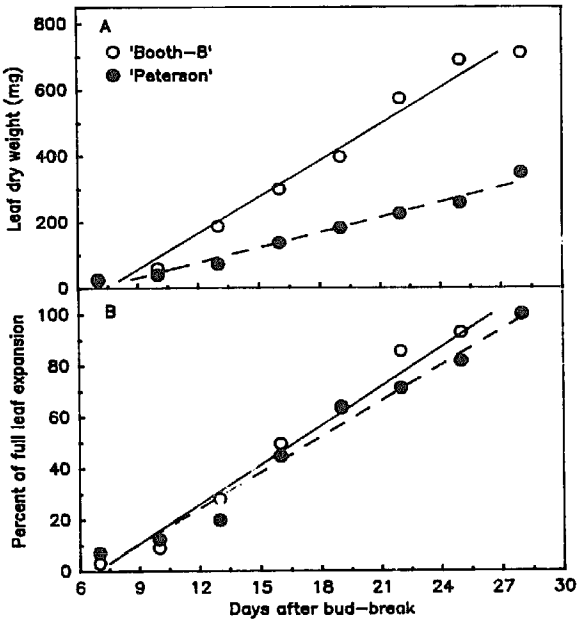

Fig. 1. Effect of leaf age on (A) leaf dry weight and (B) percentage of full leaf expansion of avocado. For leaf dry weight, the regression lines are: 'Booth-8', $y=36.4x-269.6$, $R^2=0.85$; 'Peterson', $y=15.2x-105.5$, $R^2=0.90$. For leaf expansion, the regression lines are: 'Booth-8', $y=-35.23+5.1x$, $R^2=0.98$; 'Peterson', $y=-31.19+4.46x$, $R^2=0.98$. Data points are mean values $\pm$SE, where $n=10$. In all cases, SE bars were smaller than the symbols.

RESULTS

The rate of increase in leaf dry weight was linear for both cultivars during the first 28 days after budbreak (Fig. 1(A)). Thereafter, there was no increase in leaf area and leaf dry weight for either cultivar (data not shown). However, the rate of increase and final leaf dry weight was greater for leaves of 'Booth-8' than for leaves of 'Peterson' (Fig. 1(A)). The rate of leaf expansion followed almost an identical pattern to that of leaf dry weight for both cultivars (Fig. 1(B)). The final leaf area of 'Booth-8' (101.2 cm^2) was twice as large as that of 'Peterson' (50.3 cm^2). Leaves from both cultivars reached 50% of full expansion approximately 17 days after budbreak (Fig. 1(B)). Specific leaf density remained relatively constant throughout the leaf expansion period for both cultivars as the increase in leaf area was accompanied by

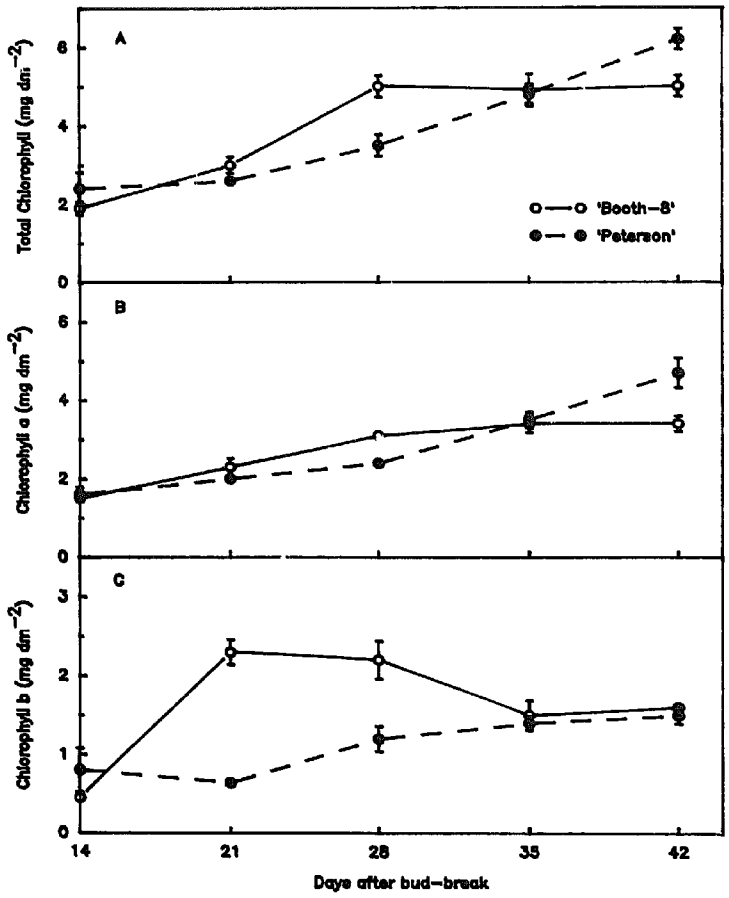

Fig. 2. Effect of leaf age on (A) total chlorophyll; (B) chlorophyll *a*, and (C) chlorophyll *b* content of 'Booth-8' and 'Peterson' avocado leaves. Data points represent means ± SE. Symbols representing means were often larger than the SE bars so that at some points the SE bars do not show.

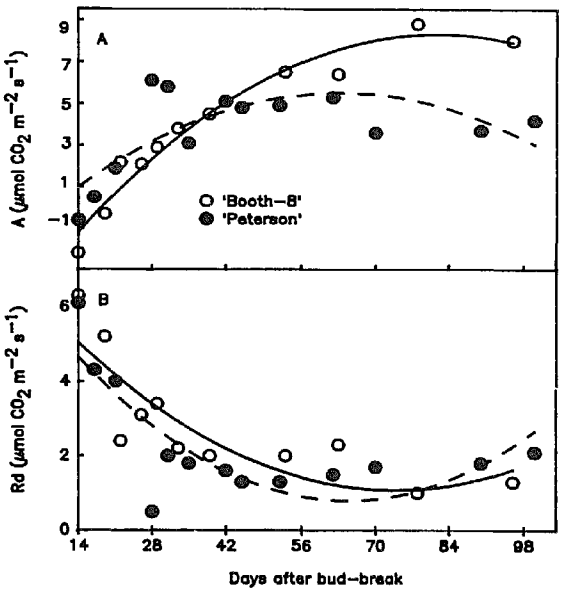

Fig. 3. Effect of leaf age on (A) net CO_2 assimilation (A) and (B) dark respiration (Rd) of avocado leaves. (A) The regression lines are: 'Booth-8', $y=-5.51+0.33x-0.0021x^2$, $R^2=0.96$; 'Peterson', $y=-1.95+0.24x-0.0018x^2$, $R^2=0.53$. (B) The regression lines are: 'Booth-8', $y=-7.1+0.16x-0.0011x^2$, $R^2=0.72$, 'Peterson', $y=-7.1+0.19x-0.0015x^2$, $R^2=0.67$. Data points are mean values where $n=15$.

an increase in leaf dry weight. Specific leaf densities averaged $6.8+0.14$ mg cm^{-2} and 6.7 ± 0.17 mg cm^{-2} for 'Booth-8' and 'Peterson', respectively.

Fourteen days after bud-break, total leaf chlorophyll content was 2.1 mg dm^{-2} for 'Booth-8' and 2.2 mg dm^{-2} for 'Peterson' (Fig. 2(A)). Total chlorophyll and chlorophyll *a* contents of 'Booth-8' leaves increased from 14 to 28 days after bud-break and remained relatively constant from 28 to 42 days after bud-break (Figs. 2(A) and 2(B)). Total chlorophyll and chlorophyll *a* contents of 'Peterson' leaves increased steadily from 21 to 42 days (Figs. 2(A) and 2(B)). Chlorophyll *b* content of 'Booth-8' leaves increased by over 300% between 14 and 21 days after bud-break, and then decreased from 28 to 35 days after bud-break (Fig. 2(C)). Chlorophyll *b* content of 'Peterson' leaves gradually increased from 21 to 35 days after bud-break (Fig. 2(C)).

Transpiration and g_s remained relatively constant for both cultivars from 14 days after bud-break to the last measurement date. From 14 days after bud-break until the end of the experiment, for 'Booth-8' and 'Peterson' mean E (pooled over time) was 7.2 ± 0.16 mmol H_2O m^{-2} s^{-1} and 8.1 ± 0.14 mmol H_2O m^{-2} s^{-1}, respectively and mean g_s (pooled over time) was 147.0 ± 4.7 mmol CO_2 m^{-2} s^{-1} and 147.2 ± 3.8 mmol CO_2 m^{-2} s^{-1}, respectively. The effect of leaf age on A was similar for both cultivars, although rates were generally higher for 'Booth-8' after leaves were fully expanded. Net CO_2 assimilation increased until about 42 days after bud-break and then leveled-off (Fig.

3(A)). Net CO_2 assimilation was only monitored for 98 days and 133 days from bud-break for 'Booth-8' and 'Peterson', respectively, owing to leaf abscission caused by an unexpected severe freeze 6 days after the last measurements. For 'Peterson', *A* began to decline 70 days after bud-break (Fig. 3(A)), and continued to decline at the same rate until 133 days after bud-break for both fruiting and non-fruiting terminals (data not shown). The effect of leaf age on *Rd* was similar for both cultivars (Fig. 3(B)). Dark respiration decreased until about 42 days after bud-break and then leveled off for 'Booth-8' and increased slightly for 'Peterson' 84 days after bud-break.

DISCUSSION

Fruit tree species differ considerably in the time required from bud-break to full leaf expansion (Hale and Weaver, 1962; Watson and Landsberg, 1979; Sams and Flore, 1982; Bongi et al., 1987). We observed that 'Peterson' and 'Booth-8' avocado leaves reached full size about 28 days after bud-break. Whiley (1990) reported a similar time from bud-break to full leaf expansion for the avocado cultivar 'Hass' (*Persea americana* var. *guatemalensis*) growing in the northeastern transval, South Africa. Net CO_2 assimilation rates of 'Booth-8' and 'Peterson' at leaf maturity were similar to those observed previously for leaves of avocado cultivar 'Booth-7' (Schaffer et al., 1987).

There was a net carbon loss (determined by summing *A* and *Rd*) from 'Booth-8' leaves until they had reached approximately 72% of their full expansion, i.e. when leaves were about 21 days old (data were not calculated for 'Peterson' owing to the poor regression fit for *A*; $R^2=0.53$; Fig. 3(A)). This compares with a net gain in *A* observed for 'Hass' leaves after they had reached 80% of their full expansion (Whiley, 1990). The slight disparity between values may be due to experimental procedures, environmental differences, or genotypic differences between cultivars drawn from the various ecophysiological races. These data are largely supported by ^{14}C translocation studies with the Mexican avocado cultivar 'Fuerte' (*P. americana* var. *drymifolia*) which suggests that the sink–source transition in avocado leaves occurs somewhere between 80 and 100% of full expansion (Blumenfeld et al., 1989).

The increase in *A* as avocado leaves matured may be attributed to an increased total chlorophyll concentration and a reduction in dark respiration. For sweet cherry, Roper and Kennedy (1986) attributed low *A* during early leaf ontogeny to increased chlorophyll concentrations. However, as leaves aged, they postulated that *A* was limited by stomatal aperture and dark reactions. Sams and Flore (1982) attributed the lower photosynthetic rate of young sour cherry leaves to immature stomates. Although stomatal density of avocado leaves is high during early leaf development (100 000 cm^{-2} at 30% full leaf expansion), they are not fully functional until the leaves are approx-

imately 90% of their full size (Scholefield and Kriedemann, 1979). However, the relatively constant g_s of avocado leaves observed in this study (data not shown) indicate that increased A was not due to increased stomatal efficiency. Owing to the very small size of the leaves and difficulty with measurements, we did not measure gas exchange prior to 14 days from bud-break. Therefore, it is possible that stomatal efficiency is related to photosynthetic efficiency of avocado leaves during early leaf ontogeny.

CONCLUSION

The data from this study indicate that avocado leaves are able to function at their physiological optimum from shortly after leaf expansion until at least 70–98 days after bud-break. This information may be useful in managing avocado canopies to maximize their photosynthetic efficiency.

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REFERENCES

Arnon, D.I., 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiol., 24: 1–15.

Blumenfeld, A., Bucholtz, A. and Erner, Y., 1989. Sink–source relationships in the partitioning of carbohydrates in avocado. ISHS International Symposium on the Culture of Subtropical and Tropical Fruits and Crops, Nelspruit, November 1989, Working Abstract 116.

Bongi, G., Mencuccini, M. and Fontanazza, G., 1987. Photosynthesis of olive leaves: Effect of light flux density, leaf age, temperature, peltates, and H_2O vapor pressure deficit on gas exchange. J. Am. Soc. Hortic. Sci., 112: 143–148.

Cannell, M.G.R., 1985. Dry matter partitioning in tree crops. In: M.G.R. Cannell and J.E. Jackson (Editors), Attributes of Trees as Crop Plants. Institute of Terrestrial Ecology, pp. 160–193.

Davenport, T.L., 1982. Avocado growth and development. Proc. Fla. State Hortic. Soc., 95: 92–96.

Hale, C.R. and Weaver, R.J., 1962. The effect of developmental stage on direction of translocation of photosynthate in *Vitis vinifera*. Hilgardia, 33: 89–131.

Kriedemann, P.E., 1968. ^{14}C translocation patterns in peach and apricot shoots. Aust. J. Agric. Res., 19: 775–780.

Leopold, A.C. and Kriedemann, P.E., 1975. Plant Growth and Development. McGraw-Hill, New York.

Malo, S.E. and Campbell, C.W., 1983. The avocado. Fruit Crops Fact Sheet FC-3, University of Florida Cooperative Extension Service, Gainesville, 4 pp.

Roper, T.R. and Kennedy, R.A., 1986. Photosynthetic characteristics during leaf development in 'Bing' sweet cherry. J. Am. Soc. Hortic. Sci., 111: 938–941.

Sams, C.E. and Flore, J.A., 1982. The influence of age, position, and environmental variables on net photosynthetic rate of sour cherry leaves. J. Am. Soc. Hortic. Sci., 107: 339–344.

Schaffer, B., Ramos, L. and Lara, S.P., 1987. Effect of fruit removal on net gas exchange of avocado leaves. HortScience, 22: 922–927.

Scholefield, P.B. and Kriedemann, P.E., 1979. Stomatal development in avocado leaves. CSIRO, Div. Hortic. Res., Rep. 1977-9, pp. 50–51.

Scholefield, P.B., Walcott, J.J., Kriedemann, P.E. and Ramadasan, A., 1980. Some environmental effects on photosynthesis and water relations of avocado leaves. Calif. Avocado Soc., Yrbk. 64: 93–105.

Venning, F.O. and Lincoln, F.B., 1958. Developmental morphology of the vegetative axis of avocado (*Persea americana* Mill.) and its significance to spacing, pruning practices and yields of the grove. Proc. Fla. State Horti. Soc., 71: 350–356.

Watson, R.L. and Landsberg, J.J., 1979. The photosynthetic characteristics of apple leaves (cv. 'Golden Delicious') during their early growth. In: R. Marcelle, H. Clijsters and M. van Poucke, (Editors), Photosynthesis and Plant Development. W. Junk, The Hague, pp. 39–48.

Whiley, A.W., 1990. CO_2 assimilation of developing fruiting shoots of cv. 'Hass' avocado (*Persea americana* Mill.) — A preliminary report. S. Afr. Avocado Growers' Assoc. Yearbk., 13, in press.

Whiley, A.W. Saranah, J.B., Cull, B.W. and Pegg, K.G., 1988. Manage avocado tree growth cycles for productivity gains. Queensland Agric. J., 114: 29–36.