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Carbon dioxide exchange of developing avocado (*Persea americana* Mill.) fruit

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Summary

Net efflux of CO_2 from attached avocado (*Persea americana* Mill.) fruit was measured periodically from three weeks after anthesis to fruit maturity. Net CO_2 exchange was determined in daylight (light respiration, R_l) at a photosynthetic photon flux (PPF) greater than 600 μmol m^{-1} s^{-1}, and in the dark (dark respiration, R_d). Dark respiration and R_l were highest during the early cell division stage of fruit growth (about 25 and 22 nmol CO_2 g_{dw}^{-1} s^{-1}, respectively) and decreased gradually until fruit maturity to about 1 and 0.5 nmol CO_2 nmol CO_2 g_{dw}^{-1} s^{-1}, respectively. Fruit photosynthesis, calculated from the difference between R_d and R_l, ranged from 0.5 to 3.1 nmol CO_2 g_{dw}^{-1} s^{-1}. Net rate of CO_2 assimilation on a fruit dry weight basis was highest during the early stages of fruit growth and reached the lowest rate at fruit maturity. Net rate of CO_2 assimilation of fruit exposed to light was 0.4 to 2.5% of that for fully expanded leaves. Although the relative amount of carbon assimilated by the fruit was small compared with the total amount of carbon assimilated by the leaves, the data indicate that avocado fruit contribute to their own carbon requirement by means of CO_2 assimilated in the light.

Introduction

Crop yield increases have been achieved largely by increasing the proportion of assimilates partitioned to the harvested organs of plants (Evans 1976). For example, in avocado (*Persea americana* Mill.), a substantial yield increase was obtained in response to a reduction in vegetative growth as a result of treatment with paclobutrazol foliar sprays (Wolstenholme et al. 1990, Whiley et al. 1991). Other key factors determining fruit yield are the respiratory cost of growth and the seasonal photosynthesis efficiency of the crop (Amthor 1984, Cannell 1985).

Respiratory losses from fleshy fruit, during growth and ripening, have been documented for several crop species (Kidd and West 1925, Jones et al. 1964, Blanke et al. 1985). However, the contribution of fruit to their own carbon economy should not be ignored. Previous studies with young green fruit have established their photosynthetic contribution to the carbon requirement for growth and maintenance (Bean and Todd 1960, Todd et al. 1961, Kriedemann 1968, Bazzaz et al. 1979, Flinn et al. 1977, Jones 1981). For example, pods of pea (*Pisum sativum*) exhibited a net photosynthetic gain during the first 30 days after anthesis, but thereafter respiration losses exceeded CO_2 assimilation (Flinn et al. 1977). For oranges and lemons (*Citrus sinensis* and *Citrus limon*), grape (*Vitis vinifera* cv. sultana), and apple (*Malus*

domestica cvs. Jonathan and Golden Delicious), fruit respiratory losses of CO_2 during a diurnal cycle exceeded photosynthetic gains throughout fruit ontogeny (Clijsters 1969, Bean et al. 1963, Kriedemann 1968, Jones 1981). However, Clijsters (1969) demonstrated a 36% reduction in the growth of apples when photosynthetic activity was inhibited by excluding light from developing fruit.

Wolstenholme (1986, 1987) calculated that the oil-accumulating avocado fruit has a high energy requirement for growth (807.2 kJ 100 g^{-1} for cv. Fuerte at 17% oil content, compared with 262.8 and 292.5 kJ 100 g^{-1} for apples and citrus, respectively). Avocado fruit are climacteric (Eaks 1980), and that respiratory sequence is initiated by detachment from the tree. Previous studies on avocado fruit respiration have been conducted exclusively with detached fruit at various stages of development and to our knowledge, there are no reports on net CO_2 exchange of avocado fruit attached to the tree throughout ontogeny. Avocado fruit remain green from setting until maturity and have a high stomatal density (50–75 stomata mm^{-2}, shortly after fruit set), with active stomata similar to those of the leaves, facilitating gas exchange (Blanke and Bower 1990). Total chlorophyll concentration in the mesocarp is only 12 to 30% that of the peel concentration (Cran and Possingham 1973). Thus, a fruit has the potential for photosynthetic activity, thereby contributing to its own carbon requirements during growth. Refixation of respiratory CO_2 within fruit by phosphoenolpyruvate carboxylase (PEPC) may be a significant contributor to fruit photosynthesis (Blanke and Lenz 1989). This mode of CO_2 refixation in fruit may also be present in avocado, because PEPC has been observed in avocado fruit (Blanke and Notton 1991).

The purpose of this study was to determine the dynamics of CO_2 efflux from avocado fruit from post anthesis to fruit maturity and to assess the contribution of fruit to their own carbon economy from the fixation of atmospheric CO_2.

Materials and methods

Avocado trees (*Persea americana* var. *americana* × *P. americana* var. *guatemalensis*, cv. Booth-7) planted at the University of Florida, Tropical Research and Education Center, Homestead, Florida (25° N latitude) were used in this study. Trees were on 'Waldin' or 'Lula' seedling rootstocks and were 35 years old at the beginning of the experiment. Trees were maintained with standard fertilization, irrigation, and pest control practices recommended for avocado (Malo and Campbell 1983).

From 3 weeks after anthesis (early April 1989) to fruit maturity (mid-September 1989), CO_2 efflux from attached fruit was determined in the field at 14-day intervals for three fruit on each of five trees. Because fruit were harvested after each measurement, different fruit were used on each measurement date. However, fruit growth rates within and among trees were fairly uniform, and flowers were tagged at anthesis to be certain that test fruit were the same age. Net CO_2 exchange of fruit was determined from CO_2 fluxes by enclosing individual small fruit in a Parkinson's leaf chamber (Analytical Development Co., Hoddesdon, Herts., England), or larger fruit in a 14 × 14 × 13 cm Plexiglas chamber containing a battery-powered fan and a

thermocouple. Net CO_2 exchange was determined with an LCA-2 field portable open gas exchange system (Analytical Development Co.) as described by Schaffer and O'Hair (1987). Flow rate of ambient air into the chamber was maintained at 400 ml min^{-1} for the first five measurement dates and at 600 ml min^{-1} for the later dates. Net CO_2 exchange was calculated using equations described by Jarvis (1971) and Von Caemmerer and Farquhar (1981). Light respiration (R_l) of fruit was determined by measuring CO_2 efflux throughout the day at a minimum photosynthetic photon flux (PPF) of 600 μmol m^{-2} s^{-1}, which exceeds the light saturation for CO_2 assimilation of avocado leaves (Scholefield et al. 1980). Immediately following measurements made in the light, the chamber was covered with two layers of black polyethylene. Dark CO_2 efflux, i.e., dark respiration (R_d), was then determined. Chamber air temperature was monitored, but not controlled, during CO_2 exchange determinations, and ranged from 31 to 45 °C during the study. Respiration data were standardized to 30 °C by using temperature response data from each sampling date. This same method has been used to standardize temperatures for peach respiration data (DeJong et al. 1987). Data were not collected until the CO_2 flux in the chamber had stabilized (about 5 minutes for small fruit during the first measurement date, and up to 2 hours for large, mature fruit). Immediately after each CO_2 exchange measurement, the fruit used was harvested and its dry weight determined after slicing and drying at 60 °C.

Fruit R_d and R_l was expressed on a g_{dw}^{-1} and a $fruit^{-1}$ basis. Statistical models determining fruit growth over time and comparing fruit dry weight to fruit R_d and R_l were constructed by linear and nonlinear regression analysis using SAS software (SAS Institute, Inc., Cary, NC, USA). Fruit photosynthetic activity was calculated from the difference between fruit R_l and fruit R_d at each point on the regression line (Bean and Todd 1960, Clijsters 1969, Jones 1981).

Light interception by the avocado tree canopy was defined in a separate study carried out on a 5-m diameter tree (cv. Hass) in subtropical southeastern Queensland (lat. 27° S). During flowering, which on avocado is mostly terminal to the last vegetative flush (Whiley et al. 1988*a*), and early fruit set, spot measurements of PPF were made with a quantum sensor (Model LI-190 SA, Li-Cor, Inc., Lincoln, NE, USA) within the fruiting zone and compared to the full sunlight position. At the completion of spring shoot growth, 1-m line sensors (Model LI-191 SA, Li-Cor, Inc.) were positioned in the fruiting zone of the tree as well as inside the canopy at distances of 0.5 and 1.0 m interior to the fruiting zone. The sensors were aligned as closely as possible to an angle of 90° to the midday sun on the northern side of the tree. A fourth quantum sensor (Model LI-190 SA, Li-Cor, Inc.) was positioned outside the tree canopy in full sunlight. The PPF was integrated hourly during the light period of each day using a datalogger (Model LI-1000, Li-Cor, Inc.) and the accumulated quanta at each line sensor expressed as a percentage of full sunlight. Mean values of the percentage of light intercepted at each point in the canopy were calculated for a 1-week period. The quantum sensors were left positioned in the tree and PPF measurements were collected again about 8 weeks later, after summer shoot growth had occurred.

Results

Fruit dry weight increased exponentially with time (Figure 1). The increase was relatively slow during the first 10 weeks after anthesis and then increased rapidly from Week 10 to fruit maturity (20 weeks after anthesis).

As fruit dry weight increased over time, R_d and R_l showed similar CO_2 efflux patterns on a dry weight basis (Figure 2a). Dark respiration and R_l were highest three weeks after anthesis, 25 and 22 nmol CO_2 g_{dw}^{-1} s^{-1}, respectively. As fruit ontogeny progressed, R_d and R_l decreased and were lowest at fruit maturity, about 1.0 and 0.5 nmol CO_2 g_{dw}^{-1} s^{-1}, respectively. The difference between R_d and R_l decreased as fruit weight increased (Figure 2a). This was concomitant with a reduction in the calculated fruit photosynthetic rate, from about 3.1 nmol CO_2 g_{dw}^{-1} s^{-1} during early fruit growth to about 0.5 nmol CO_2 g_{dw}^{-1} s^{-1} at fruit maturity (Figure 2b).

The pattern of fruit respiration expressed on a per fruit basis was similar in the dark and the light (Figure 3a). Until fruit dry weight reached 10 g, R_d and R_l per fruit increased linearly as the fruit developed (Figure 3a). When fruit were about one-third of their mature weight (20 g dry weight), respiration per fruit approached an asymptote and increased little until fruit were harvested (Figure 3a). Dark respiration was always greater than R_l, and these differences were greatest when fruit dry weight was between 20 and 55 g (Figure 3a). Respiration rates were highest at fruit maturity and were about 208 and 152 nmol CO_2 $fruit^{-1}$ s^{-1} or 34 and 25 mg CO_2 h^{-1} for R_d and R_l, respectively. Calculated fruit photosynthesis, expressed on a per fruit basis, increased linearly as fruit dry weight increased from 0 to 20 g, then leveled off when fruit reached approximately half of their maturation weight (Figure 3b). There was little increase in calculated fruit photosynthesis as fruit weight increased from 30 to 60 g.

Photosynthetic photon flux measurements taken during flowering and early fruit

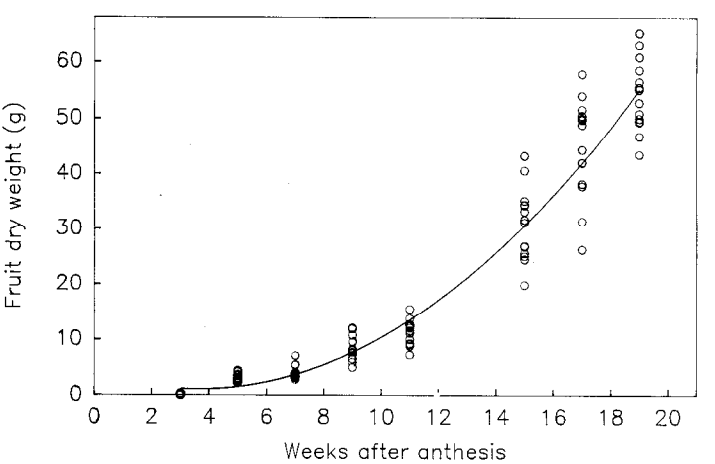

Figure 1. Fruit dry weight of 'Booth-7' avocados during fruit development. The regression line is defined by the equation: $y = 3.94 - 1.618x + 0.227x^2$, $R^2 = 0.99$.

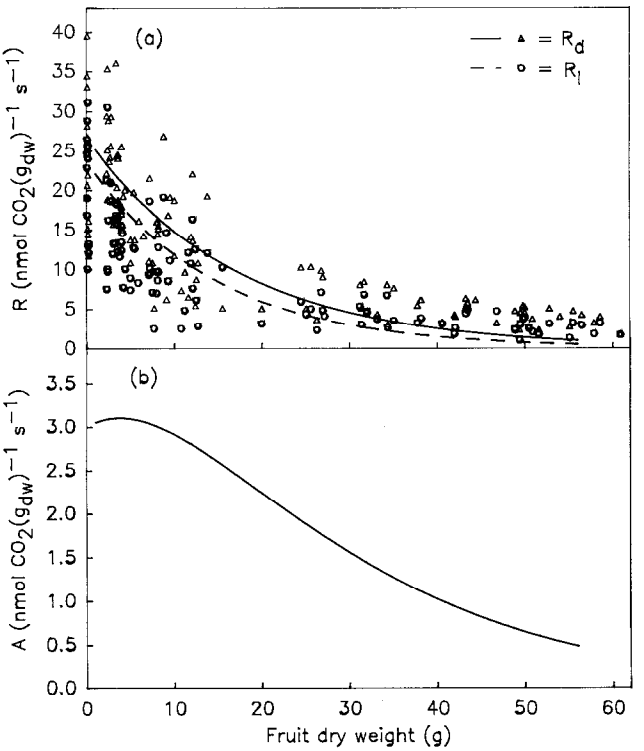

Figure 2. (a) Respiration of developing 'Booth-7' avocado fruit in the dark (R_d) and in the light (R_l) expressed on a gram dry weight basis, where the regression line for R_d is defined by the equation: $y = 26.55e^{-0.057x}$, $R^2 = 0.60$, and the regression line for R_l is defined by the equation: $y = 19.98e^{-0.0067x}$, $R^2 = 0.63$. (b) Net CO_2 assimilation (A), determined from $R_d - R_l$ of developing 'Booth-7' avocado fruit, expressed on a gram dry weight basis.

set indicated that most young fruit were exposed to full sunlight for the first four weeks of their development (data not shown). During the two periods when light interception data were integrated, daily PPF ranged from 15.5 mol m^{-2} on overcast days to 59.5 mol m^{-2} on cloud-free days. By the end of spring shoot growth, light transmission to the fruiting zone had been reduced to 35.9% of full sunlight, and at distances of 0.5 and 1.0 m inside the canopy from the fruiting zone it had been reduced to 13.7 and 9.7%, respectively (Figure 4). By the end of the summer shoot growth, light transmission to the fruiting zone had further declined to 13.1% of full sunlight and to 9.7 and 6.3% of the respective internal monitoring positions.

Discussion

The dynamics of R_d and R_l observed for attached, developing avocado fruit were similar to those observed for other crops (Clijsters 1969, Jones et al. 1964, Jones 1981, DeJong et al. 1987, DeJong and Walton 1989). The highest respiration rates were observed during the early stage of fruit growth, from the first measurement date

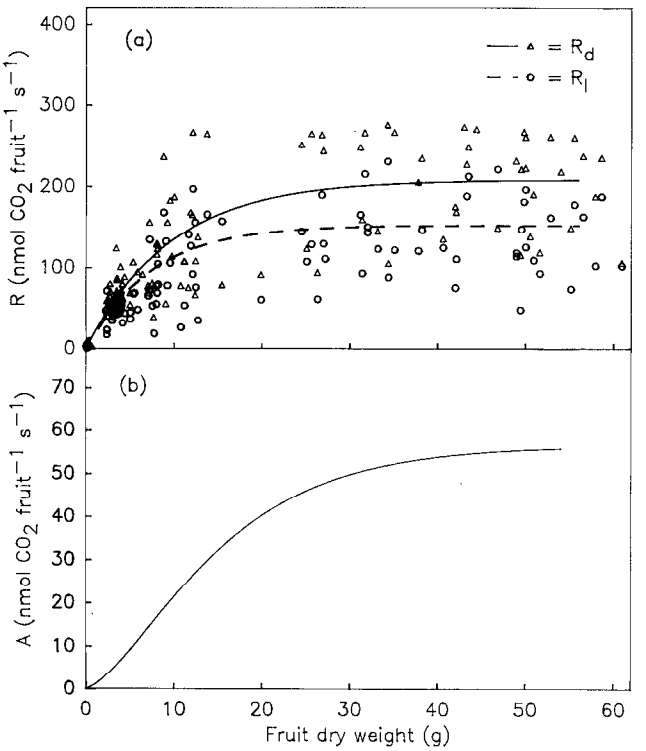

Figure 3. (a) Fruit respiration of developing 'Booth-7' fruit in the dark (R_d) and in the light (R_l) expressed on a $fruit^{-1}$ basis, where the regression line for R_d is defined by the equation: $y = 209.01\ (1 - e^{-0.107x})$, $R_2 = 0.71$, and the regression line for R_l is defined by the equation: $y = 140.60(1 - e^{-0.117x})$, $R^2 = 0.66$. (b) Net CO_2 assimilation (A), determined from $R_d - R_l$ of developing 'Booth-7' avocado fruit, expressed on a per fruit basis.

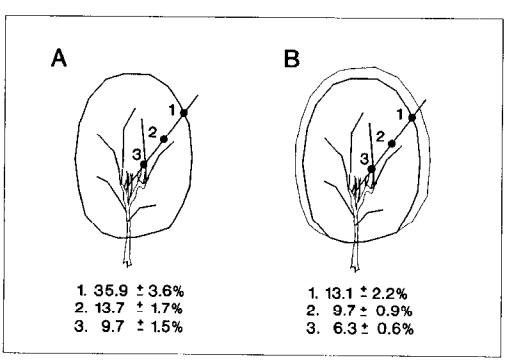

Figure 4. Light transmission in an avocado tree canopy: (A) when spring shoot growth had stopped and (B) at the end of summer shoot growth. Photosynthetic photon flux (PPF) was measured in full sunlight, (1) in the fruiting zone, (2) 0.5 m interior to the fruiting zone and (3) 1.0 m interior to the fruiting zone. Data are mean values ± SE ($n = 7$) of the percentage of full sunlight measured at each point. The PPF in full sunlight ranged between 15.5 and 56.6 mol m^{-2} (A) and 19.8 to 59.5 mol m^{-2} (B) over each 7-day period.

to about 12 weeks after anthesis, then decreased to the lowest rates at fruit maturity. The period when the highest respiration rates were observed corresponds to the time that cell division is greatest in avocado fruit (Valmayor 1967). Similar patterns have been reported previously for avocado (Todd et al. 1961), apple (Clijsters 1969, Jones 1981) and peach (DeJong et al. 1987, DeJong and Walton 1989). The maximum R_d value measured at 30 °C for avocado fruit of about 25 nmol CO_2 g_{dw}^{-1} s^{-1} was similar to R_d measured at 20 °C for apple fruit, about 26 nmol CO_2 g_{dw}^{-1} s^{-1} (recalculated from Jones 1981) and peach fruit at 20 °C, about 28 nmol CO_2 g_{dw}^{-1} s^{-1} (DeJong et al. 1987). Jones (1981) reported that the greatest difference between R_d and R_l for apple was during the early phase of fruit growth and the smallest difference was at fruit maturation. We observed a similar response for avocado fruit. When the R_d and R_l of avocado were expressed on a per fruit basis, respiration at 30 °C was highest at fruit maturity, about 34 and 25 mg CO_2 h^{-1} $fruit^{-1}$ for R_d and R_l, respectively. These values were somewhat lower than the value of 50 mg CO_2 h^{-1} $fruit^{-1}$ measured at 23 °C reported for avocado by Blanke (1991). The difference between values may be due to experimental or genotypic differences. The cultivar used in Blanke's (1991) study was *P. americana* var. *drymifolia* cv. Fuerte, whereas we used the hybrid *P. americana* var. *americana* × *P. americana* var. *guatemalensis* cv. Booth-7. The oil concentration of 'Booth-7' fruit (about 8%) is lower than that of 'Fuerte' (about 12–14%) at maturity (C.W. Campbell, personal communication). Presumably this leads to lower energy demands for growth and development for 'Booth-7' than for 'Fuerte' (Wolstenholme 1986), resulting in lower respiratory activity in 'Booth-7' fruit.

At all stages of fruit development, fruit photosynthesis was substantially less than dark respiration. However, the calculated photosynthetic rate of developing avocado fruit (i.e., the difference between R_d and R_l; Todd et al. 1961, Jones 1981), was highest during early fruit growth, about 3.0 nmol CO_2 g_{dw}^{-1} s^{-1}. The photosynthetic rates for developing avocado fruit were 42 times less than those for mature leaves, about 126.0 nmol CO_2 g_{dw}^{-1} s^{-1} (Schaffer and Whiley, unpublished data).

Although chlorophyll concentrations in the peel of avocado fruit are similar to concentrations in the leaves (Cran and Possingham 1973, Schaffer et al. 1991), the difference in the maximum CO_2 assimilation rates between the two organs may be attributed to the difference in the chlorophyll a/b ratio, which is 1–2/1 in fruit (Cran and Possingham 1973) and 2–3.3/1 in leaves (Schaffer et al. 1991). However, the difference in the amount of CO_2 assimilated between the organs is more likely to be a result of the greater surface area to volume ratio in leaves than in fruit, which results in a severe decline of light penetration into fruit tissue (only 0.02% of incident light penetrates more than 2 mm into an avocado fruit (Cran and Possingham 1973)), and a change in the spectrum of photosynthetically active radiation (Blanke 1990). This relationship is further expressed by the declining net CO_2 assimilation (expressed as nmol CO_2 g_{dw}^{-1} s^{-1}) as fruit increase in size.

Vu et al. (1985) suggested that reproductive organs fix little atmospheric CO_2 by means of ribulose-bisphosphate carboxylase (RuBPC) in the respiratory pentose phosphate (RPP) pathway. They reported that the CO_2 assimilation (PEPC/RuBPC)

ratio was 4–5/1 and 0.1/1 for citrus flowers and leaves, respectively. Furthermore, Blanke and Lenz (1989), Blanke (1990), and Blanke and Notton (1991) concluded that refixation of respiratory CO_2 by the PEPC pathway provides a significant contribution of carbon by the fruit for its own growth requirements. The data from the present study indicate that avocado fruit contribute to their own carbon requirement by means of CO_2 fixation in the light and that the relative contribution of fruit photosynthesis to the total energy requirement is greatest during the early stages of fruit development. This may be a significant factor influencing fruit retention because it is concomitant with the period of photoassimilate competition between reproductive and vegetative sinks (Biran 1979, Blumenfeld et al. 1983, Wolstenholme et al. 1990, Whiley et al. 1991), which extends for about 42 days after spring shoot growth commences (Whiley 1990). In addition, the over-wintered leaf canopy has lost photosynthetic efficiency (Whiley, unpublished data) at a time of critical assimilate demand. During this period young developing fruit are in full sunlight with the opportunity to maximize their photoassimilate contributions to growth. Our data show that up to the end of spring shoot growth, when fruit have attained a size between 12 and 15 g dry weight, there is sufficient light during cloud-free conditions to support fruit photosynthesis within the fruiting zone of the canopy. However, by the time the summer growth flush is complete (Whiley et al. 1988*b*), the light environment in the fruiting zone is unlikely to support photosynthetic activity in the fruit. At this stage of fruit ontogeny the renewed and photosynthetically efficient leaf canopy would meet all photoassimilate requirements of fruit growth.

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