

Effects of leaf, shoot and fruit development on photosynthesis of lychee trees (*Litchi chinensis*)

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Summary Changes in gas exchange with leaf age and fruit growth were determined in lychee trees (*Litchi chinensis* Sonn.) growing in subtropical Queensland (27° S). Leaves expanded in a sigmoid pattern over 50 days during spring, with net CO₂ assimilation (*A*) increasing from -4.1 ± 0.9 to $8.3 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ as the leaves changed from soft and red, to soft and light green, to hard and dark green. Over the same period, dark respiration (*R_d*) decreased from 5.0 ± 0.8 to $2.0 \pm 0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Net CO₂ assimilation was above zero about 30 days after leaf emergence or when the leaves were half fully expanded. Chlorophyll concentrations increased from $0.7 \pm 0.2 \text{ mg g}^{-1}$ in young red leaves to $10.3 \pm 0.7 \text{ mg g}^{-1}$ in dark green leaves, along with stomatal conductance (*g_s*, from 0.16 ± 0.09 to $0.47 \pm 0.17 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$).

Fruit growth was sigmoidal, with maximum values of fresh mass (29 g), dry mass (6 g) and fruit surface area (39 cm²) occurring 97 to 115 days after fruit set. Fruit CO₂ exchange in the light (*R_l*) and dark (*R_d*) decreased from fruit set to fruit maturity, whether expressed on a surface area (10 to 3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and 20 to 3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively) or on a dry mass basis (24 to 2 $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ and 33 to 2 $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$, respectively). Photosynthesis never exceeded respiration, however, the difference between *R_l* and *R_d* was greatest in young green fruit (4 to 8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). About 90% of the carbon required for fruit growth was accounted for in the dry matter of the fruit, with the remainder required for respiration. Fruit photosynthesis contributed about 3% of the total carbon requirement of the fruit over the season. Fruit growth was mainly dependent on CO₂ assimilation in recently expanded dark green leaves.

Keywords: carbon balance, chlorophyll, fruit growth, gas exchange, leaf age, *Litchi chinensis*, respiration.

Introduction

Leaves are the main source of photosynthesis in plants, but CO₂ assimilation can also take place in stems, flowers and fruit. Photosynthetic rates are generally low in young unex-

panded leaves, and increase up to full leaf expansion or soon after the leaves become fully expanded (Kramer and Kozlowski 1979, Flore and Lakso 1989). This phase of leaf development may take several days or weeks. Kennedy and Johnson (1981) studied gas exchange in expanding leaves of apple, (*Malus domestica* L.) over a single season and found that net CO₂ assimilation increased from 5 to 25 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ as the leaves expanded from a plastochron index of 4 (5% of final leaf size) to 10 (70% of final leaf size). Leaf expansion was also accompanied by increases in stomatal conductance (*g_s*) and carboxylation efficiency.

The surface layers of many fruits contain chlorophyll, and can fix carbon when exposed to sunlight (Blanke and Lenz 1989). Stomata are also present in the outer layer of many fruits, but usually with only 1 to 10% of the frequency compared with leaves of the same species. The number of stomata is set at anthesis and remains constant, hence stomatal frequency decreases as the fruit expands. The relative rate of CO₂ fixation is greatest during early fruit development, and declines as the fruit matures (e.g., in apple (Blanke and Lenz 1989) and in avocado (*Persea americana* Mill.; Whiley et al. 1992)). The contribution of fruit photosynthesis to reproductive growth varies across species, environment and fruit type, but ranges from 5 to 15% for many fruit trees (Birkhold et al. 1992, Pavel and DeJong 1993, Marcellis and Baan Hofman-Eijer 1995).

We report on the relationships between photosynthesis and leaf and fruit development in lychee (*Litchi chinensis* Sonn.), a tropical evergreen tree from the rainforests of southeast Asia. Fruits are born on terminal shoots, with the new leaves and stems growing in a series of flushes (about six to eight leaves), with dormant periods between successive flushes. We hypothesized that maximum rates of CO₂ assimilation occur only in fully expanded leaves. We also studied seasonal changes in light (*R_l*) and dark respiration (*R_d*) of fruit from a few weeks after anthesis until harvest, to test the hypothesis that lychee fruits make a significant contribution to their growth only when they are small and green.

Materials and methods

Leaf growth and gas exchange over time

Gas exchange was measured in 10-year-old “Bengal” lychee trees growing in the field at Nambour in subtropical Australia (27° S) from August 7 to September 19, 1998. The relationship between length of the central vein in a leaflet (L_{length} , 5 to 190 mm) and leaf area (L_{area} , cm²) established for orchard trees was used in Equation 1 to calculate total leaf area from the combined areas of the leaflets from each leaf:

$$L_{\text{area}} = 234.8 / (1 + (L_{\text{length}} / 319.5)^{-1.86}) \quad (1)$$

$$r^2 = 0.98; P < 0.001; n = 313.$$

Young leaves in the middle position of terminal flushes were tagged, and leaf area and net CO₂ assimilation (A) were recorded every 3 to 4 days from leaf unfolding to full expansion between 0830 and 1000 h with an LI-6200 photosynthesis system (Li-Cor, Lincoln, NE), equipped with a 1-l chamber. Gas exchange of the growing leaves was compared with that of a set of fully expanded, dark green control leaves. Temperature in the chamber was 27 ± 3 °C, vapor pressure deficit (VPD) was 1 ± 0.5 kPa, and photosynthetic photon flux density (PPFD) was above $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. Values presented are the means of six leaves from two trees per sampling period.

Leaf growth was described by a modified logistic model (Hieke et al. 2002a). On each measurement day, middle leaves from a separate set of flushes of the same age as the leaves used for the gas exchange measurements were harvested and their fresh and dry masses determined. Before the leaves were dried, chlorophyll concentrations were determined with a chlorophyll meter (Model SPAD-502, Minolta, Japan). The relationship between leaf chlorophyll concentration (Chl, mg g⁻¹ fresh leaf weight) and SPAD readings (S) was established as: $\text{Chl } a + b = 0.027S^{1.56}$, $r^2 = 0.94$, $P < 0.001$. Values presented are means (\pm SE) of six leaves ($n = 3$ for controls).

Gas exchange during stages of leaf development

To assess the impact on A of any changes in growing conditions that may have occurred between August 7 and September 19, 1998, we measured A and dark respiration (R_d) between 0830 and 1000 h over 7 days in September 1998 on the middle leaf of a range of terminal shoots of the same trees sampled in the previous study. Temperature in the chamber was 29 ± 2 °C, VPD was 1 ± 0.5 kPa and PPFD was above $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. Gross photosynthesis (P_g) was calculated by summing A and R_d . Shoot elongation and leaf expansion were recorded on additional sets of corresponding flushes, to estimate the age of leaves used for the gas exchange measurements. Values presented are the means of six leaves per leaf stage from two trees. Leaf stage was equivalent to time since leaf emergence: Stage 1, soft red, Day 18; Stage 2, red brown, Day 27; Stage 3, green brown, Day 32; Stage 4, light green, Day 39; Stage 5, green soft, Day 44; and Stage 6, dark green, Day 49. Growth of shoots and leaves ($n = 6$) was described by a modified logistic model (Hieke et al. 2002a).

Fruit gas exchange

Experiments were conducted on 8-year-old “Wai Chee” lychee trees from November 24, 1995 to January 14, 1996 (Year 1), on 6-year-old “Kwai May Pink” trees from November 13, 1996 to January 29, 1997 (Year 2) and on 10-year-old “Kwai May Pink” trees from October 20, 1998 to January 22, 1999 (Year 3) near Nambour. The first measurements were made 2 to 4 weeks after fruit set. Measurements were stopped when fruits were considered commercially mature, about a week before maximum fruit weight. The cultivar “Bengal” did not crop during this period.

Efflux of CO₂ from attached sunlit fruit was determined in the field at 1- or 2-week intervals for three fruits on each of four or five trees ($n = 12$ or 15). Because fruits were harvested after each measurement to record their weight and size, different fruits were used on each date. Net CO₂ exchange of fruits was determined with a Li-Cor LI-6200 portable photosynthesis meter. Light respiration (R_l) of fruit was monitored at a minimum PPFD of $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ and an ambient CO₂ concentration of about 350 ppm. Immediately following measurements in the light, the chamber was covered with black, light-proof material. Dark respiration (R_d) was then measured after CO₂ flux in the chamber had stabilized. Measurements were taken between 0800 and 1000 h, with earlier measurements later in the season, to reduce the impact of increasing temperatures on respiration rates. Chamber air temperature was monitored, but not controlled during the measurements, and generally ranged between 28 and 32 °C.

Immediately after CO₂ measurement, fruits were harvested, and length, width, and fresh and dry biomass (oven-dried at 60 °C for 10 days) determined. Fruit surface area (F_{area}) was calculated based on the formulas for a prolate sphere for small fruit, and an oblate sphere for more mature fruit (Turrell 1946). Fruit CO₂ exchange in light and dark was calculated per unit surface area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and per unit dry mass (nmol CO₂ g⁻¹ s⁻¹). Gross fruit photosynthesis (P_g) was calculated from the difference between R_l and R_d for each measurement (Whiley et al. 1992). A carbon balance was constructed by calculating total respiration (R_{total}) (Equation 2) and total gross fruit photosynthesis ($P_{g,\text{total}}$) (Equation 3) per fruit per day (Bazzaz and Carlson 1979) expressed in mg carbon (C) and converting fruit dry mass to carbon equivalents by multiplying by 0.436, the experimentally determined ratio of g C per g dry weight for barley tops (Biscoe et al. 1975; the molecular weight ratio of C in one carbohydrate molecule C₆H₁₀O₅ is 0.444).

$$R_{\text{total}} = (R_{d(30^\circ\text{C})} \times 14 \text{ h} + R_{d(20^\circ\text{C})} / 2 \times 10 \text{ h}) \text{ dry weight.} \quad (2)$$

Nighttime respiration (R_d) (20 °C) was calculated from respiration measured during the day (30 °C), assuming a Q_{10} of 2 (Lloyd et al. 1995) and a mean day temperature of 30 °C and a mean night temperature of 20 °C.

$$P_{g,\text{total}} = ((R_d - R_l) 14 \text{ h}) \text{ dry weight.} \quad (3)$$

To convert assimilation rate from $\mu\text{mol CO}_2 \text{ fruit}^{-1} \text{ s}^{-1}$ to $\text{mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}$, values were multiplied by 158.4 and divided by the dry mass ($\mu\text{mol CO}_2 \text{ fruit}^{-1} \text{ s}^{-1} = 44 \times 3600/1000 \text{ mg CO}_2 \text{ g}^{-1} \text{ h}^{-1}/\text{dry mass}$). The equivalent carbon content (C , $\text{mg g}^{-1} \text{ h}^{-1}$) was calculated by dividing by 3.6 ($\text{CO}_2/C = 44/12 = 3.6$). Total carbon requirement was calculated as the sum of the cumulative total respiration per day from fruit set, and the carbon equivalent of fruit dry mass. The total contribution of fruit photosynthesis to fruit carbon requirement was estimated by summing total daily gross photosynthesis from fruit set. Fruit growth and CO_2 exchange over time were subjected to regression analysis, based on values for 12 or 15 fruits.

Results

Leaf growth and gas exchange over time

In spring, leaves took about 30 days to reach 50% of maximum area and 50 days to reach 100% of maximum area (Figure 1). Increases in dry mass, like those in area, followed a sigmoidal growth curve. Mean solar radiation was $15 \pm 1 \text{ MJ m}^{-2} \text{ day}^{-1}$, and mean maximum and minimum air temperatures were $27.4 \pm 0.5 \text{ }^\circ\text{C}$ and $13.9 \pm 0.5 \text{ }^\circ\text{C}$, respectively.

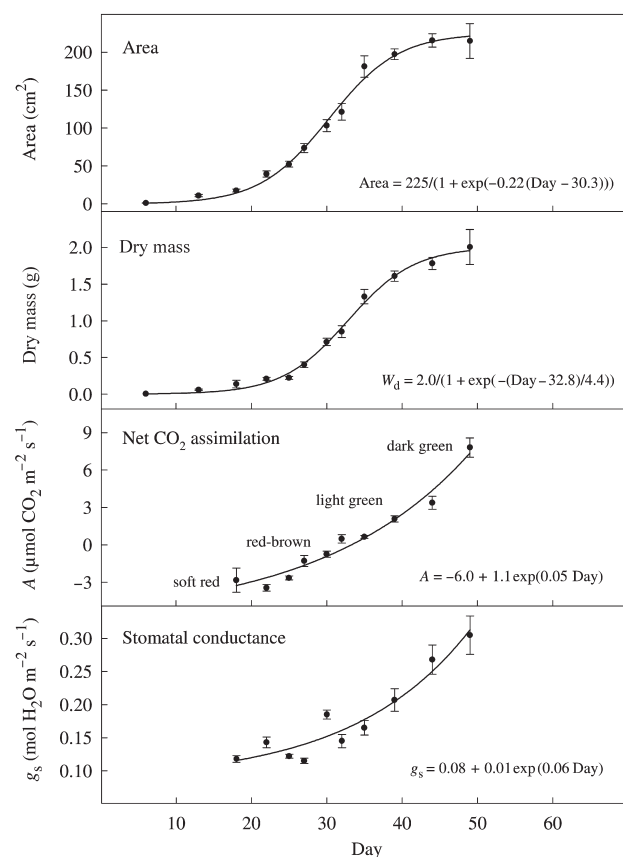


Figure 1. Changes in area, dry mass (W_d), net CO_2 assimilation (A) and stomatal conductance (g_s) during leaf development in “Bengal” lychee. Values are means (\pm SE) of six leaves. Appearance of leaves is indicated for A . For regressions, $r^2 = 0.99$ and $P < 0.001$, except for A ($r^2 = 0.97$) and g_s ($r^2 = 0.92$).

Table 1. Changes in leaf color and chlorophyll concentration ($\text{mg per g fresh mass}$) during leaf development in “Bengal” lychee. Data are the means (\pm SE) of six leaves.

Leaf stage	Leaf area (% final area)	Leaf color	Chlorophyll concentration ($\text{mg g}_{\text{fm}}^{-1}$)
One	24	Red	0.5 ± 0.1
Two	56	Red-brown	2.3 ± 0.1
Three	84	Green-brown	3.3 ± 0.1
Four	92	Light green	4.4 ± 0.1
Five	100	Green, soft	5.7 ± 0.1
Six	100	Dark green, hardened	9.6 ± 0.4

Net CO_2 assimilation (A) per unit leaf area increased exponentially as the leaves expanded and changed appearance (Figure 1). The increase in A was associated with increased chlorophyll concentrations (Table 1) and higher g_s (Figure 1), but lower internal CO_2 concentrations (data not presented). When the data were related to leaf area expansion, the increase in gas exchange was directly related to the proportion of final leaf area (Figure 2). There was also an increase in A after maximum leaf expansion, as the leaves hardened and turned dark green. The increase in A during leaf maturation was strongly related to changes in g_s and chlorophyll concentration (Figure 3).

Gas exchange during leaf development

Shoots elongated over 30 days and leaves expanded over

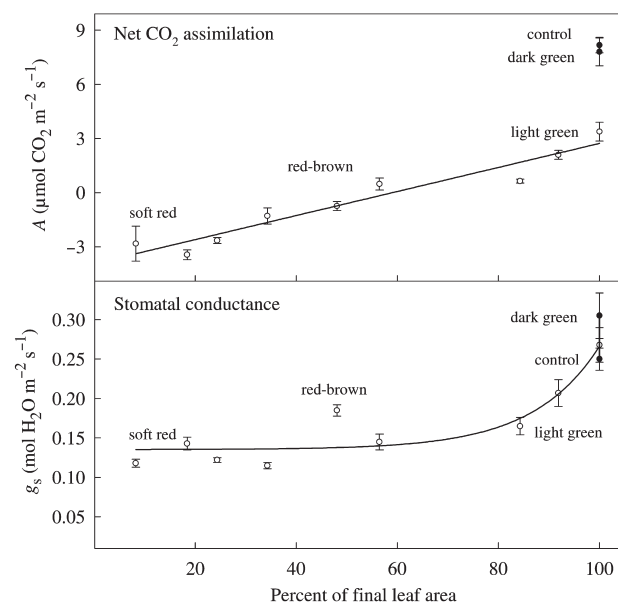


Figure 2. Relationships between net CO_2 assimilation (A), stomatal conductance (g_s) and leaf area (L_{area}) in “Bengal” lychee. The appearance of leaves is indicated. Values are means (\pm SE) of six leaves per leaf stage, except for control ($n = 30$). Regressions are: $A = -3.9 + 0.07L_{\text{area}}$ ($r^2 = 0.93$, $P < 0.001$); and $g_s = 0.14 + \exp(0.08L_{\text{area}})$ ($r^2 = 0.83$, $P < 0.005$). Dark green and control leaves were not included in the regressions.

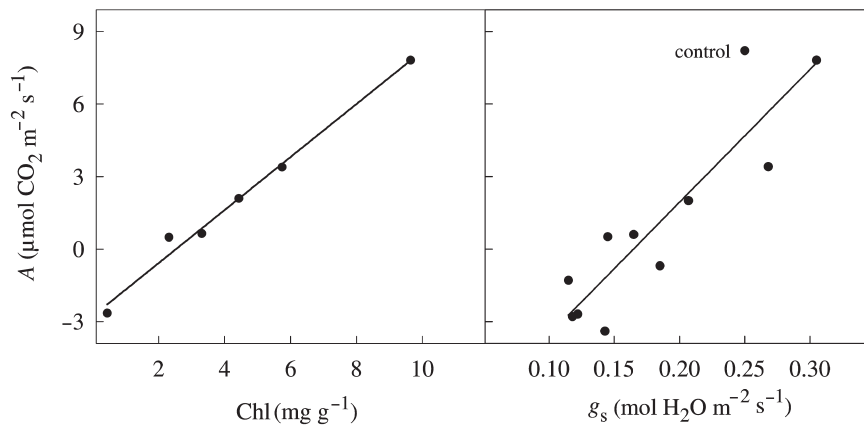


Figure 3. Relationships between net CO_2 assimilation (A) and chlorophyll concentration (Chl) and stomatal conductance (g_s) with leaf development in "Bengal" lychee. Values are means of six leaves per leaf stage. Regressions are: $A = -2.8 + 1.1\text{Chl}$ ($r^2 = 0.99$, $P < 0.001$); and $A = -9.0 + 54.9g_s$ ($r^2 = 0.81$, $P < 0.001$). Control leaves included in regression for g_s .

60 days (Figure 4). The leaf measured for gas exchange in position four on the flush emerged about 10 days after the first leaf and also took about 30 days to develop. Net CO_2 assimilation increased exponentially as leaves reached full expansion and changed from red to light green (Figure 5). There was also an increase in A as the leaves hardened and turned dark green. In contrast, R_d decreased as the leaves changed from soft red to light green. Based on these data, we calculated a P_g of about $2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in young leaves and $11 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in mature leaves (Figure 5).

Fruit gas exchange

Fruits were harvested after 113 days in Year 1, 97 days in Year 2 and 115 days in Year 3. Because the responses were similar over the 3 years, only data for one year are presented (Figure 6). Until about 70 to 84 days after fruit set, fruits were longer than wide (prolate spheres), however as the fruits matured, they became wider, approximating the shape of oblate spheres.

Fruit CO_2 exchange in the light and dark on a surface area or dry mass basis decreased over time: it was highest in young fruit (Figure 6) and remained low 70 days after fruit set. The data for R_d and R_l expressed on a surface area or dry mass basis over time fitted an exponential decay curve ($f = a\exp(-bx)$; r^2 between 0.88 and 0.99, $P < 0.001$).

Dark respiration was higher than R_l during early fruit development, when the fruits were green and contained chlorophyll. About 63 to 70 days after fruit set, fruits turned yellow-red and there was no difference between R_d and R_l . Gross photosynthesis (P_g) of developing fruits, calculated as the difference between R_d and R_l (Todd et al. 1961, Jones 1981), was always less than R_d . However, P_g was highest during early development at $8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ or $13 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ (Figure 6). The two cultivars were similar, with mean P_g of $6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ or $10 \text{ nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ during early development in all 3 years. Gross photosynthesis (P_g) was describe by fitting a sigmoidal curve ($f = a/(1 + \exp(-(x - c)/b))$).

The relative costs for respiration and dry matter can be used to estimate fruit carbon utilization efficiency (DeJong and Walton 1989). About 90% of the carbon was used for fruit growth ($89.2 \pm 1.2\%$, mean of 3 years), whereas about 10%

was used for respiration ($10.8 \pm 1.2\%$). The contribution of the fruit to its own growth was greatest when fruits were young and declined as they matured. Over the whole season, fruit P_g contributed only $2.8 \pm 0.4\%$ to the total carbon requirement of the fruit.

Discussion

Leaves did not begin to contribute to the carbon economy of the plant until they were about half fully expanded, and did not reach maximum rates of photosynthesis until after they were fully expanded and dark green. Fruit were able to contribute to their growth only while they were still green and less than 3 g dry mass. Dark green, fully expanded leaves of the recent flushes were the main contributors to lychee fruit growth.

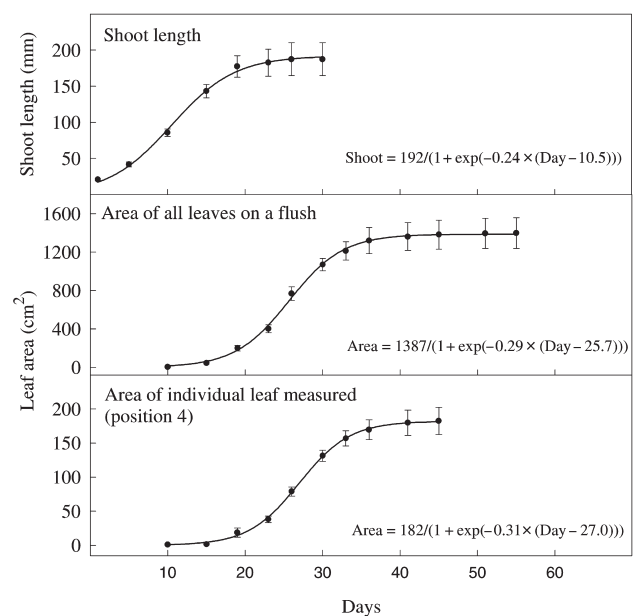


Figure 4. Changes in shoot elongation and leaf area during leaf development in "Bengal" lychee. Photosynthesis was measured on the fourth leaf of terminal shoots of other branches growing at the same time (see Figure 5). Values are means (\pm SE) of six shoots. For regressions, $r^2 = 0.99$ and $P < 0.001$.

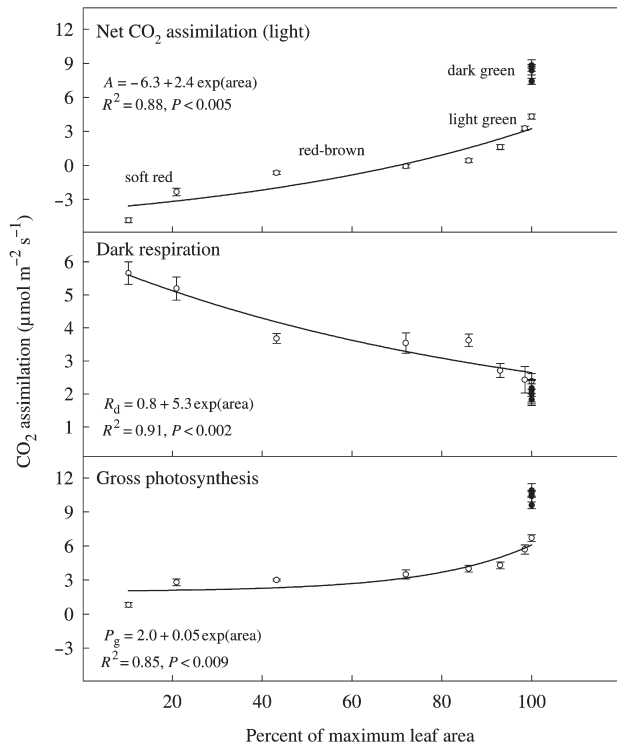


Figure 5. Relationships between net CO_2 assimilation (A), dark respiration (R_d), gross photosynthesis (P_g), and leaf expansion in “Bengal” lychee. Gas exchange was measured over 7 days in September on leaf four of terminal shoots. Shoots were sampled to give a range in leaf area. Leaf area development was monitored on other shoots growing at the same time (see Figure 4). Appearance of leaves indicated. Values are means (\pm SE) of six leaves per leaf stage. Dark green leaves were not included in the regressions.

Changes in CO_2 assimilation with leaf age

Net CO_2 assimilation was negative in small leaves, rose above zero when they were about 30 days old or 50% of their final size, and did not reach a maximum until after the leaves were fully expanded and dark green. These new leaves had similar rates of photosynthesis as the older dark green leaves from the previous flush. Hieke et al. (2002b) studied the relationship between CO_2 assimilation and irradiance and showed that maximum A of leaves was similar in lychee cultivars “Kwai May Pink” and “Salathiel” ($12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

Development of shoot growth, leaf expansion and photosynthesis in lychee is similar to that in other tropical evergreen trees such as avocado (Schaffer et al. 1991), cashew (*Anacardium occidentale* L.) and mango (*Mangifera indica* L.). Schaper and Chacko (1993) studied gas exchange and leaf development in cashew in northern Australia, and reported that leaves reached full size 25 days after they emerged, but maximum A did not occur until after 50 days. Photosynthesis then remained high for another 150 days. Nii et al. (1995) examined the development of mango leaves in Japan, and found that green, immature but fully expanded leaves had lower A ($3.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than mature, fully expanded leaves ($4.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), indicating that photosynthesis lagged

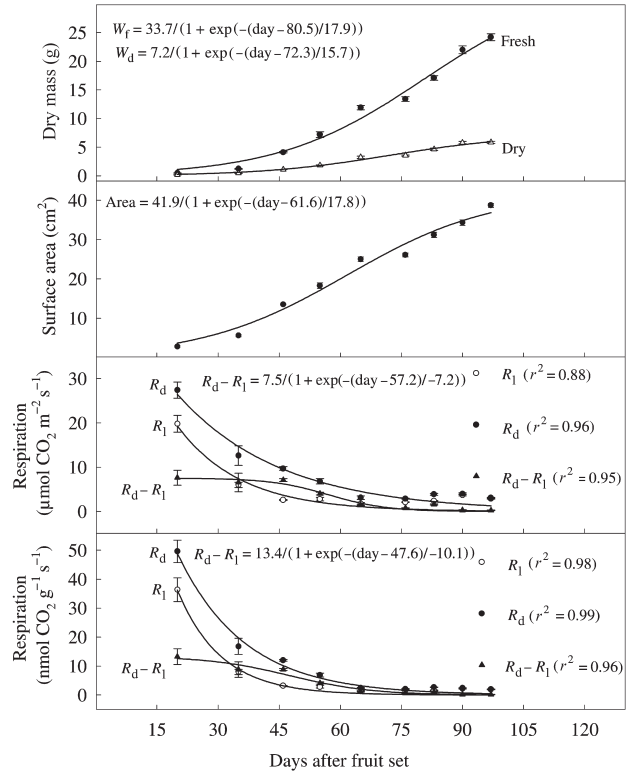


Figure 6. Fruit growth and respiration of “Kwai May Pink” lychee in Year 2 expressed per surface area and dry weight. Values are means (\pm SE) of 12 fruits. For regressions, $r^2 > 0.98$ and $P < 0.001$ for fruit growth.

behind leaf expansion. In contrast, in temperate deciduous trees such as apple, maximum rates of photosynthesis generally occurred at the time of maximum leaf expansion or sometime before (Kennedy and Johnson 1981).

Export of assimilates from young leaves

In young expanding leaves, R_d exceeded P_g . Net CO_2 assimilation rose above zero only when the leaves were about 30 days old or half of their final size. Leaves of temperate deciduous trees typically begin to export assimilates at a much earlier stage of development than leaves from tropical evergreen trees. The leaves of temperate deciduous trees only live for a few months, whereas leaves from tropical trees may persist for several years. Johnson and Lakso (1986) reported that CO_2 assimilation in “Jonamac” apple was above zero at 20% of full leaf expansion, with smaller basal leaves (1 cm^2) on a shoot supplying carbohydrates to the rest of the shoot shortly after emergence. Schaffer et al. (1991) studied gas exchange in field-grown avocado trees in Florida, and reported that A became positive about 17 days after bud break or 72% leaf expansion. These data are similar to results obtained from ^{14}C studies showing transition from sink to source when the leaves were 80% fully expanded (Blumenfield et al. 1989, cited in Schaffer et al. 1991). In lychee, once newly expanded leaves turned dark green, A was similar to that of older dark green leaves from the previous flush. In other studies in lychee (au-

thors' unpublished data), yield of trees with all old leaves removed was 35% lower than that of undefoliated controls, whereas yield of trees with the last and the previous flush removed was 45% lower than that of undefoliated controls. These data indicate that most of the photosynthates required for lychee fruit growth come from recently fully expanded dark green leaves.

Relationships between net CO₂ assimilation, chlorophyll concentrations and stomata

The increase in *A* as the leaves developed was strongly related to increases in *g_s* and chlorophyll concentration, which were highest in dark green leaves. Thus, gas exchange followed the course of chlorophyll synthesis, which lagged behind leaf expansion. This response is typical for many tropical evergreens (Schaffer et al. 1991, Schaper and Chacko 1993, and Nii et al. 1995). Photosynthesis of mango leaves was generally below zero across a range of PPFD values in immature, chocolate-colored and light chocolate-colored leaves, and above zero in green, immature and mature leaves (Nii et al. 1995). The green immature leaves were fully expanded, indicating that new shoots begin to export assimilates to the rest of the tree much later than in temperate species. There are also good correlations between photosynthesis and chlorophyll concentrations in temperate trees (Kennedy and Johnson 1981), although maximum values are reached at or before full leaf expansion.

Pattern of fruit gas exchange

Similar patterns of CO₂ exchange expressed on a fruit mass or surface area basis have been reported for other species. The highest *R_d* values (mean of 3 years) for young lychees were about 20% higher than those recorded for avocado (Whiley et al. 1992), apple (Jones 1981) and peach (*Prunus persica* L.; DeJong et al. 1987). Fruit photosynthesis was highest during early development, at 6 μmol CO₂ m⁻² s⁻¹ or about 10 nmol CO₂ g⁻¹ s⁻¹. Whiley et al. (1992) reported a reduction in *P_g* from 3 nmol CO₂ g⁻¹ s⁻¹ when fruit had a dry mass of 5 g to 0.5 nmol CO₂ g⁻¹ s⁻¹ when fruit had a dry mass of 55 g.

Contribution of fruit photosynthesis

The contribution of fruit photosynthesis to the total carbon requirement of a fruit was highest during early development and declined to zero at harvest. The fruit contributed 3% to its own carbon requirement over the season. About 90% of the carbon required for growth could be accounted for in the dry matter of the fruit itself, with the remainder needed for respiration. These values are close to the mean value of 80% estimated for peach (DeJong and Walton 1989). Pavel and DeJong (1993) reported that photosynthesis of peach provided 3 to 9% of the weekly carbohydrate requirements early in the season and 8 to 15% mid-season, whereas mature fruits contributed only 3 to 5% of their carbohydrate requirements. In lychee, calculated *P_g* never compensated for *R_d*, however *P_g* was highest during early fruit growth.

In conclusion, lychee fruits obtain the carbohydrates needed for growth from photosynthesis in the green fruit itself or from photosynthesis in the leaves. Fruit photosynthesis contributed less than 5% of the carbon needed for fruit growth. Changes in gas exchange with leaf development indicated that most of the photosynthates required for fruit growth came from recently fully expanded, dark green leaves.

References

- Bazzaz, F.A. and R.W. Carlson. 1979. Photosynthetic contribution of flowers and seeds to reproductive effort of an annual colonizer. *New Phytol.* 82:223–232.
- Birkhold, K.T., K.E. Koch and R.L. Darnell. 1992. Carbon and nitrogen economy of developing rabbiteye blueberry fruit. *J. Am. Soc. Hort. Sci.* 117:139–145.
- Biscoe, P.V., J.N. Gallagher, E.J. Littleton, J.L. Monteith and R.K. Scott. 1975. Barley and its environment. 4. Sources of assimilate for the grain. *J. App. Ecol.* 12:295–318.
- Blanke, M.M. and F. Lenz. 1989. Fruit photosynthesis. *Plant Cell Environ.* 12:31–46.
- DeJong, T.M. and E.F. Walton. 1989. Carbohydrate requirements of peach fruit growth and respiration. *Tree Physiol.* 5:329–335.
- DeJong, T.M., J.F. Doyle and K.R. Day. 1987. Seasonal patterns of reproductive and vegetative sink activity in early and late maturing peach (*Prunus persica*) cultivars. *Physiol. Plant.* 71:83–88.
- Flore, J.A. and A.N. Lakso. 1989. Environmental and physiological regulation of photosynthesis in fruit crops. *Hort. Rev.* 11:111–157.
- Hieke, S., C.M. Menzel and P. Lüdders. 2002a. Shoot development, chlorophyll, gas exchange and carbohydrates in lychee seedlings (*Litchi chinensis*). *Tree Physiol.* 22:947–953.
- Hieke, S., C.M. Menzel and P. Lüdders. 2002b. The effects of photosynthetic photon flux density on leaf gas exchange and leaf expansion in lychee (*Litchi chinensis*). *Tree Physiol.* In Press.
- Johnson, R.S. and A.N. Lakso. 1986. Carbon balance model of a growing apple shoot: I. Development of the model. *J. Am. Soc. Hort. Sci.* 111:160–164.
- Jones, H.G. 1981. Carbon dioxide exchange of developing apple (*Malus pumila* Mill.) fruits. *J. Exp. Bot.* 32:1203–1210.
- Kennedy, R.A. and D. Johnson. 1981. Changes in photosynthetic characteristic during leaf development in apple. *Photosynth. Res.* 2:213–223.
- Kramer, P.J. and T.T. Kozlowski. 1979. *Physiology of woody plants.* Academic Press, New York, 811 p.
- Lloyd, J., S.C. Wong, J.M. Styles, D. Batten, R. Priddle, C. Turnbull and C.A. McConchie. 1995. Measuring and modelling whole-tree gas exchange. *Aust. J. Plant Physiol.* 22:987–1000.
- Marcelis, L.E.M. and L.R. Baan Hofman-Eijer. 1995. The contribution of fruit photosynthesis to the carbon requirement of cucumber fruit as affected by irradiance, temperature and ontogeny. *Physiol. Plant.* 93:476–483.
- Nii, N., N.T. Watanabe, K. Yamaguchi and M. Nishimura. 1995. Changes of anatomical features, photosynthesis and ribulose biphosphate carboxylase-oxygenase content of mango leaves. *Ann. Bot.* 76:649–656.
- Pavel, E.W. and T.M. DeJong. 1993. Estimating the photosynthetic contribution of developing peach (*Prunus persica*) fruits to their growth and maintenance carbohydrate requirements. *Physiol. Plant.* 88:331–338.
- Schaffer, B., A.W. Whiley and R.R. Kholi. 1991. Effects of leaf age on gas exchange characteristics of avocado (*Persea americana* Mill.). *Sci. Hort.* 48:21–28.

- Schaper, H. and E.K. Chacko. 1993. Effect of irradiance, leaf age, chlorophyll content and branch-girdling on gas exchange of cashew (*Anacardium occidentale* L.) leaves. *J. Hort. Sci.* 68: 541–550.
- Todd, G.W., R.C. Bean and B. Probst. 1961. Photosynthesis and respiration in developing fruits. II. Comparative rates at various stages of development. *Plant Physiol.* 36:69–73.
- Turrell, F.M. 1946. Tables of surfaces and volumes of spheres and of prolate and oblate spheroids, and spheroidal coefficients. University of California Press, Berkeley, 153 p.
- Whiley, A.W., B. Schaffer and S.P. Lara. 1992. Carbon dioxide exchange of developing avocado (*Persea americana* Mill.) fruit. *Tree Physiol.* 11:85–94.