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Effects of light availability on leaf gas exchange and expansion in lychee (*Litchi chinensis*)

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Summary Effects of photosynthetic photon flux density (PPFD) on leaf gas exchange of lychee (*Litchi chinensis* Sonn.) were studied in field-grown "Kwai May Pink" and "Salathiel" orchard trees and young potted "Kwai May Pink" plants during summer in subtropical Queensland (27° S). Variations in PPFD were achieved by shading the trees or plants 1 h before measurement at 0800 h. In a second experiment, potted seedlings of "Kwai May Pink" were grown in a heated greenhouse in 20% of full sun (equivalent to maximum noon PPFD of 200 μmol m^{-2} s^{-1}) and their growth over three flush cycles was compared with seedlings grown in full sun (1080 μmol m^{-2} s^{-1}). Young potted plants of "Kwai May Pink" were also grown outdoors in artificial shade that provided 20, 40, 70 or 100% of full sun (equivalent to maximum PPFDs of 500, 900, 1400 and 2000 μmol m^{-2} s^{-1}) and measured for shoot extension and leaf area development over one flush cycle.

Net CO_2 assimilation increased asymptotically in response to increasing PPFD in both orchard trees and young potted plants. Maximum rates of CO_2 assimilation (11.9 ± 0.5 versus 6.3 ± 0.2 μmol CO_2 m^{-2} s^{-1}), dark respiration (1.7 ± 0.3 versus 0.6 ± 0.2 μmol CO_2 m^{-2} s^{-1}), quantum yield (0.042 ± 0.005 versus 0.027 ± 0.003 mol CO_2 mol^{-1}) and light saturation point (1155 versus 959 μmol m^{-2} s^{-1}) were higher in orchard trees than in young potted plants. In potted seedlings grown in a heated greenhouse, shoots and leaves exposed to full sun expanded in a sigmoidal pattern to 69 ± 12 mm and 497 ± 105 cm^2 for each flush, compared with 27 ± 7 mm and 189 ± 88 cm^2 in shaded seedlings. Shaded seedlings were smaller and had higher shoot:root ratios (3.7 versus 3.1) than seedlings grown in full sun. In the potted plants grown outdoors in 20, 40, 70 or 100% of full sun, final leaf area per shoot was 44 ± 1, 143 ± 3, 251 ± 7 and 362 ± 8 cm^2, respectively. Shoots were also shorter in plants grown in shade than in plants grown in full sun (66 ± 5 mm versus 101 ± 2 mm).

Photosynthesis in individual leaves of lychee appeared to be saturated at about half full sun, whereas maximum leaf expansion occurred at higher PPFDs. We conclude that lychee plants can persist as seedlings on the forest floor, but require high PPFDs for optimum growth.

Keywords: leaf growth, light compensation, photosynthetic photon flux density, photosynthesis models, saturation point, shade.

Introduction

Lychee (*Litchi chinensis* Sonn.) is native to subtropical rainforests of southern China and northern Vietnam, but is now cultivated in much of South-East Asia and in parts of Australia, America, Africa and the Mediterranean (Menzel and Simpson 1990, 1994). Rainforest surveys have shown that wild trees grow in abundance on Hainan Island mainly at elevations of 600 to 800 m, and below 500 m in mountainous areas in Leizhou Peninsula and in the west of Guangdong and east of Guangxi Provinces. Lychees are the predominant species in several of these areas and may comprise up to 50% of the virgin forests. Some of these trees are 30 m tall, with a girth of 2 m, and have well-developed buttress roots. Because of the economic value of lychee fruits, there is interest in determining the physiology of this tropical species so that management techniques can be devised to maximize fruit yields.

Between 1 and 2% of the solar radiation falling on Earth's surface is used by plants to fix CO_2 in photosynthesis (Turner 1994). The amount of CO_2 fixed by a tree depends on the distribution of light through the canopy and the physiology of the leaves, especially their nitrogen content. Several studies have investigated the photosynthetic responses of tropical tree seedlings to changes in solar radiation (Thompson et al. 1988, Ramos and Grace 1990, Riddoch et al. 1991, Wiebel et al. 1993, Eschenbach et al. 1998). For example, Riddoch et al. (1991) reported that photosynthesis in *Nauclea diderrichi* Merrill, a West African pioneer tree, was saturated at a photosynthetic photon flux density (PPFD) of 1000 μmol m^{-2} s^{-1}, whereas in the climax species, *Entandrophragma angolense* (Welw.) C. DC., photosynthesis saturated at a PPFD of 300 μmol m^{-2} s^{-1}. Seedlings of the climax species presumably fixed significant amounts of CO_2 at PPFDs commonly found in small gaps in the forest understory. There have been relatively few studies on South-East Asian rainforest species in situ (Eschenbach et al. 1998) because most studies of tropical tree species have used young seedlings in containers.

The effects of PPFD on leaf expansion were studied over 30 years ago in non-woody plants such as cucumber (*Cucumis sativus* L.; Milthorpe and Newton 1963, Newton 1963, Wilson 1966), but there have been few studies on tropical trees. Shade had no effect on shoot growth of potted avocado (*Persea americana* Mill.; Chirachint and Turner 1988), whereas full sun stunted the growth of seedlings of the understory mangosteen tree (*Garcinia mangostana* L.) compared with seedlings grown in 50 or 80% of full sun (Wiebel et al. 1994). Similarly, shading resulted in increased leaf area in citrus (*Citrus paradisi* Pers.) and carambola (*Averrhoa carambola* L.; Syvertsen and Smith 1984, Marler et al. 1994).

The effects of PPFD on gas exchange of two cultivars of orchard-grown lychee in subtropical Australia were studied. The response of orchard trees was compared with that of young plants growing nearby in small pots. We hypothesized that field trees would have higher dark respiration (R_d), light compensation point, apparent quantum yield (ϕ), light saturated CO_2 assimilation (A_{max}) and light saturation point ($PPFD_{sat}$) than potted plants. The effects of PPFD on leaf growth and dry matter production of pot-grown plants were also investigated. The hypothesis that low PPFDs reduce total plant dry mass and expansion of individual leaves was tested as well.

Materials and methods

Leaf gas exchange of field-grown trees and potted plants

Experiments were conducted on 3-year-old lychee trees of "Kwai May Pink" and "Salathiel" growing in an orchard and on 2-year-old potted "Kwai May Pink" plants nearby at Nambour in subtropical Queensland (27° S). The potted plants were grown outdoors under ambient conditions in 10-l pots containing a 2:1:1 (v/v) sand:peat:soil mix, and were fertilized and watered regularly. Both groups of plants ($n = 6$) produced new shoots over summer, even though the potted plants had restricted root growth in the containers.

Measurements of gas exchange were made at 0800 h on clear and overcast days on a fully mature leaf behind the growth flush, with an LI-6200 photosynthesis meter (Li-Cor, Lincoln, NE) equipped with a 1-l chamber. Frames covered with shade cloth were placed next to the orchard trees or potted plants to provide a range of PPFDs 1 h before net CO_2 assimilation (A), stomatal conductance (g_s) and internal CO_2 concentration (C_i) were measured. A set of full sun plants was used as controls. Maximum PPFD was 2300 μmol m^{-2} s^{-1}. Determinations of A in the dark were obtained by covering the chamber with black light-proof material. Dark respiration was measured after CO_2 flux in the chamber had stabilized. Data were collected from January 11 to March 16, 2000. During the measurements, mean air temperature in the chamber in full sun was 30 ± 0.5 °C and vapor pressure of the air (VP) was 1.9 ± 0.1 kPa. Ambient CO_2 concentrations were about 350 ppm.

Data were subjected to regression analysis using SigmaPlot Version 4 software (Jandel Scientific, San Rafael, CA):

$$A = A_{max}(1 - \exp(-b\mathrm{PPFD})), \tag{1}$$

where A is net CO_2 assimilation, PPFD is photosynthetic photon flux density and b is a constant.

We also modeled changes in A by fitting data to two nonrectangular hyperbolas, using the nonlinear least squares curve fitting program of SigmaPlot (Jandel Scientific). Equation 2 has been used to assess photosynthesis in needles of conifer trees (*Picea* spp. and *Pinus sylvestris* L.) and leaves of sweetgum (*Liquidambar styraciflua* L.; Leverenz 1987, Herrick and Thomas 1999).

$$\begin{aligned} A = {} & (\mathrm{PPFD}\phi + A_{max} - ((\mathrm{PPFD}\phi + A_{max})^2 \\ & - 4\mathrm{PPFD}\phi A_{max}\varphi)^{0.5}) / (2\varphi), \end{aligned} \tag{2}$$

where ϕ is apparent quantum yield or photosynthetic efficiency, A_{max} is light-saturated net CO_2 assimilation and φ describes the convexity of the curve. Convexity varies from one, when the curve is of the Blackman type, to zero, when the response is a rectangular hyperbola (Leverenz 1987).

Equation 3 has been used to describe the relationship between A and PPFD in northern red oak seedlings (*Quercus rubra* L.; Hanson et al. 1987).

$$A = A_{max}\left(1 - \left(\frac{1 - R_d}{A_{max}}\right)\right)\exp\left(\frac{1 - x}{\mathrm{PPFD}_{comp}}\right), \tag{3}$$

where PPFD_{comp} is the PPFD when $A = R_d$ (light compensation point).

The value of PPFD_{sat} was calculated as the PPFD associated with 90% of A_{max}. The PPFD associated with a 50% reduction in A_{max} ($\mathrm{PPFD}_{50\%}$) was also calculated. Light compensation point (where $A = R_d$) and ϕ were calculated from plots of A versus PPFD between 0 and 100 μmol m^{-2} s^{-1} (Leverenz 1987). Changes in g_s and C_i with PPFD were modeled by regression analysis ($n = 180$ for "Kwai May Pink" orchard trees, $n = 200$ for "Salathiel" orchard trees and $n = 100$ for potted plants).

Effect of light on growth of potted seedlings in a greenhouse

Experiments were conducted on 18-month-old "Wai Chee" seedlings grown in 4-l pots containing sand, peat and soil (2:1:1, v/v) in a heated greenhouse with day/night temperatures of 30 ± 4/22 ± 4 °C and a VP of 0.5 to 1.5 kPa during the day. The seedlings were fertilized every 2 to 4 weeks with a nutrient solution containing (mmol liter^{-1}): N, 14; P, 2.4; and K, 4.3; and (μmol) S, 20; Mg, 21; Mn, 4.5; Fe, 17.9; Zn, 0.8; Cu, 0.8; and B, 9.1. The seedlings were also given a foliar spray containing 0.2 g l^{-1} each of Mg, Zn and Cu every month.

The relationship between length of the central vein in a leaflet (L, 10 to 150 mm) and leaf area (L_{area}, cm^2) established for greenhouse-grown seedlings was used (Hieke et al. 2002).

Growth of seedlings under shade cloth transmitting 20% of full sunlight (equivalent to maximum noon PPFD of 200 μmol m^{-2} s^{-1}) was studied over three flushing cycles, in July, September and November 1996. These seedlings were compared with a set of controls grown in unshaded plots with a maximum PPFD of 1080 μmol m^{-2} s^{-1}. Every 2 or 3 days, shoot extension (S_{length}) and L_{area} were determined. Growth of the shoots and leaves was described by a modified logistic model (Hieke et al. 2002) (Equations 4 and 5).

$$S_{\text{length}} = S_{\max} / (1 + \exp(-k(t - m))) , \tag{4}$$

$$L_{\text{area}} = L_{\max} / (1 + \exp(-k(t - m))), \tag{5}$$

where $S_{\max}$ is maximum shoot length (mm), $L_{\max}$ is maximum area of the leaves (cm^2), k is a rate constant (day^{-1}), m describes the time to reach maximum growth rate, and t is time in days. This model was fitted to the growth data using the iterative process of the Marquardt-Levenberg algorithm. Values are presented as means (± SE) for each day.

At the end of the experiment, the plants were divided into leaves, stems and roots, dried at 60 °C and weighed. The shoot:root ratio was determined from the ratio of dry mass between above- and belowground plant parts. Values are presented as treatment means (± SE) ($n = 8$).

Effect of light on growth of potted plants raised outdoors

Experiments were conducted on 2-year-old “Kwai May Pink” plants grown outdoors at Nambour in 10-l pots containing sand, peat and soil (2:1:1), and fertilized and watered regularly. Shade cloth was placed over groups of plants on June 3, 1997 to provide irradiances of 20, 40 or 70% of full sun (equivalent to maximum PPFDs of 500, 900 and 1400 μmol m^{-2} s^{-1}). A set of unshaded controls grown in full sun received maximum PPFDs at noon of 2000 μmol m^{-2} s^{-1}. All plants produced new shoots at the start of the experiment. Shoot extension and leaf area were determined weekly over one flush cycle from June to September 1997. All plants produced flower panicles at the end of measurements. A modified logistic model (Hieke et al. 2002) described the growth of the shoots and leaves. Values are presented as means (± SE) of eight plants per treatment.

Results

Leaf gas exchange of field-grown trees and potted plants

Relationships between A and PPFDs between 0 and 100 μmol mol^{-2} s^{-1} are shown in Figure 1. Parameters R_d and ϕ were slightly lower in potted plants than in orchard trees (Table 1). The light compensation point calculated for the “Salathiel” trees was low, possibly because of errors in the calculation of assimilation at low PPFDs when the CO_2 uptake rate is close to the respiration rate.

Figure 2 shows the light responses of the orchard trees and potted plants defined by exponential curves with $r^2 > 0.87$ and $P < 0.001$. Maximum CO_2 assimilation was similar in the two cultivars in the orchard (Table 1), with the potted plants having only 50% of the $A_{\max}$ values of the orchard trees. The PPFD required to saturate photosynthesis (PPFD associated with 90% of $A_{\max}$) in potted plants was 83% of the mean $PPFD_{\text{sat}}$ for orchard trees. Net CO_2 assimilation was essentially independent of PPFDs greater than 960 μmol m^{-2} s^{-1} in potted plants and greater than 1150 μmol m^{-2} s^{-1} in orchard trees. The PPFD associated with a 50% reduction in maximum photosynthesis ($PPFD_{50\%}$) was slightly higher in the orchard trees than in the potted plants (Table 1). Mean A and g_s were higher in the orchard trees than in the potted plants (Table 1), but there was no relationship between g_s and PPFD ($r^2 < 0.28$). Low values of g_s were recorded at low and high PPFDs.

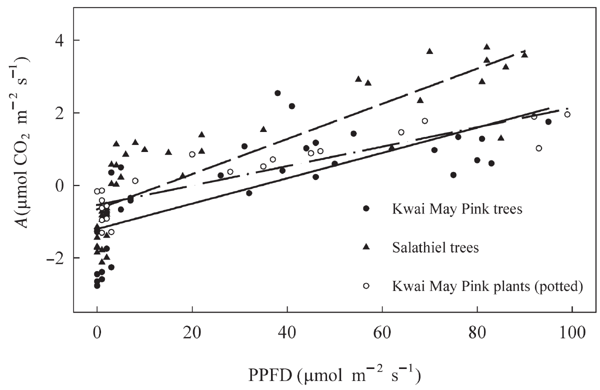

Figure 1. Effects of PPFD from 0 to 100 μmol m^{-2} s^{-1} on net CO_2 assimilation (A) of “Kwai May Pink” orchard trees ($A = -1.20 + 0.035\text{PPFD}$; $r^2 = 0.53$, $P < 0.001$, $n = 33$), “Salathiel” orchard trees ($A = -0.66 + 0.048\text{PPFD}$; $r^2 = 0.76$, $P < 0.001$, $n = 42$), and potted “Kwai May Pink” plants ($A = -0.54 + 0.027\text{PPFD}$; $r^2 = 0.80$, $P < 0.001$, $n = 22$). Quantum yields (ϕ) were calculated from the slope of the regressions. Light compensation point is the PPFD when $A = R_d$.

There was a slight exponential decline in C_i as PPFD increased from 0 to 2200 μmol m^{-2} s^{-1} (Figure 2). In full sun, minimum C_i fell to 280 ppm in the orchard trees compared with 310 ppm in the potted plants. Lower C_i in the leaves of orchard trees was associated with higher mean g_s and A. These results suggest that light effects on leaf chemistry are more important than light effects on stomata ($r^2 < 0.28$ for g_s versus PPFD). Stomatal conductance was a poor indicator of potential CO_2 assimilation ($r^2 < 0.14$).

Leaf temperature increased from 25 to 32 °C in the orchard trees and from 30 to 34 °C in the potted plants as PPFD increased from 0 to 2200 μmol m^{-2} s^{-1}. Vapor pressure of the air increased by 0.2 to 0.4 kPa with the increase in PPFD. In contrast, increases in VPD between the leaf and air (difference between the saturated leaf and the drier air above the leaf) with PPFD were 0.80 kPa for the potted “Kwai May Pink” plants, 0.83 kPa for the “Kwai May Pink” orchard trees and 0.80 kPa for the “Salathiel” orchard trees. There was no relationship ($r^2 > 0.37$) between gas exchange (A or g_s) and temperature under either overcast or clear sky conditions.

Table 1. Summary of gas exchange parameters of lychee trees and plants. Parameters R_d (dark respiration), mean A (net CO_2 assimilation), mean g_s (stomatal conductance) and mean C_i (internal CO_2 concentration) were calculated from measured data (n = 180 to 200). Quantum yield (ϕ) and light compensation point were calculated from A versus PPFD (photosynthetic photon flux density) (0–100 µmol m^{-2} s^{-1}) (n = 22 to 42). Parameters A_{max}, $PPFD_{sat}$ and $PPFD_{50\%}$ were calculated from A versus PPFD (0–2200 µmol m^{-2} s^{-1}) based on the exponential model.

Parameters	Method of determination	Field-grown "Kwai May Pink" trees	Field-grown "Salathiel" trees	Pot-grown "Kwai May Pink" plants
R_d (µmol CO_2 m^{-2} s^{-1})	Measured data	2.1 ± 0.3	1.3 ± 0.1	0.6 ± 0.2
ϕ (mol CO_2 mol^{-1})	Figure 1	0.035 ± 0.004	0.048 ± 0.004	0.027 ± 0.003
Light compensation point (µmol m^{-2} s^{-1})	Figure 1	34	14	20
A_{max} (µmol CO_2 m^{-2} s^{-1})	Equation 1	12.6 ± 0.3	11.2 ± 0.2	6.3 ± 0.2
$PPFD_{sat}$ (µmol m^{-2} s^{-1})	Equation 1	1214	1096	959
$PPFD_{50\%}$ (µmol m^{-2} s^{-1})	Equation 1	367	329	289
Mean A (µmol CO_2 m^{-2} s^{-1})	Measured data	7.1 ± 0.4	6.1 ± 0.3	3.6 ± 0.3
Mean g_s (mol H_2O m^{-2} s^{-1})	Measured data	0.90 ± 0.03	0.93 ± 0.03	0.50 ± 0.02
Mean C_i (ppm)	Measured data	313 ± 2	310 ± 2	325 ± 1

Effect of light on growth of potted seedlings in a greenhouse

Seedlings in the heated greenhouse flushed three times between July and December (Figure 3). Shoots of the control and shaded seedlings exhibited a sigmoid growth pattern and took 28 to 38 days to reach a mean length of 69 ± 12 mm and 27 ± 7 mm, respectively. With increasing solar radiation from Cycle 1 (mean of 6 ± 1 MJ m^{-2} day^{-1}) to Cycle 2 (mean of 9 ± 1 MJ m^{-2} day^{-1}) and Cycle 3 (mean of 11 ± 1 MJ m^{-2} day^{-1}), leaf expansion took 50 days in Cycle 1 compared with 35 days in Cycles 2 and 3. Mean leaf area per seedling was 497 ± 105 cm^2 in full sun compared with 189 ± 88 cm^2 in shaded seedlings. Rates of stem extension and leaf expansion were lower in the controls than in the shaded seedlings (higher m), except for leaf expansion in Cycle 2. The empirical model by Hieke et al. (2002) fitted the data well ($r^2 > 0.96$; $P < 0.001$).

The shade treatment (20% of full sunlight) reduced total seedling dry mass by 42% (13.9 ± 2.7 g versus 23.9 ± 2.0 g), with a greater response in roots (2.9 ± 0.4 g versus 5.9 ± 0.6 g) than in leaves (6.8 ± 1.4 g versus 11.0 ± 0.9 g) or stems (4.2 ± 0.9 g versus 7.1 ± 0.7 g), so that the shoot:root ratio was higher in seedlings grown in shade than in full sun (3.7 ± 0.3 versus 3.1 ± 0.1). There was a strong relationship between stem, root and total seedling mass, and leaf dry mass across the two treatments (Figure 4), indicating that leaf dry mass was a good indicator of seedling biomass in both full sun and shade.

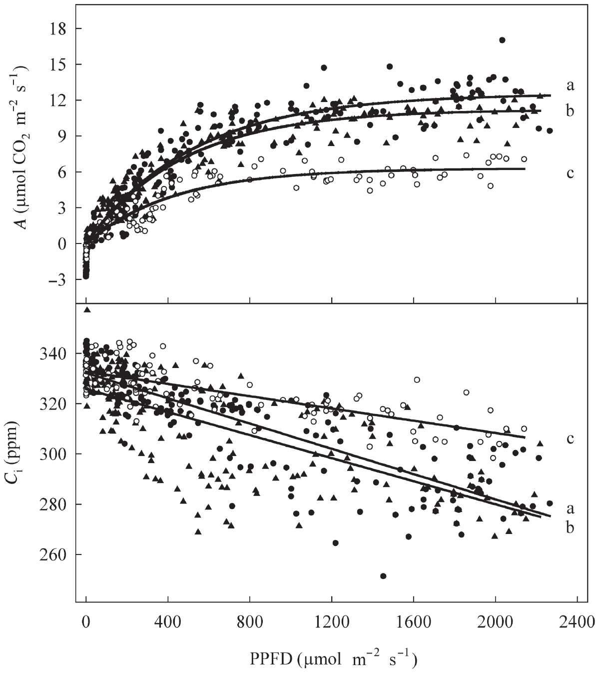

Figure 2. Effects of PPFD on net CO_2 assimilation (A) and internal CO_2 concentration (C_i) of "Kwai May Pink" (a) and "Salathiel" (b) orchard trees, and potted "Kwai May Pink" (c) plants. Regressions are A = 12.6(1 – exp(–0.002PPFD)) (r^2 = 0.90, P < 0.001, n = 180) and C_i = 270.4 + 66.5exp(–0.0007PPFD) (r^2 = 0.73, P < 0.001) for "Kwai May Pink" trees; A = 11.2(1 – exp(–0.002PPFD)) (r^2 = 0.90, P < 0.001, n = 200) and C_i = 287.5 + 46.9exp(–0.0018PPFD) (r^2 = 0.60, P < 0.001) for "Salathiel" trees; and A = 6.3(1 – exp(–0.002PPFD)) (r^2 = 0.87, P < 0.001, n = 100) and C_i = 231.1 + 102.0exp(–0.0001PPFD) (r^2 = 0.56, P < 0.001) for potted "Kwai May Pink" plants.

Effect of light on growth of potted plants raised outdoors

Growth of shoots and leaves of the potted plants raised outdoors was sigmoidal in full sun and shade (Figure 5). During June to September, when mean maximum and minimum air temperatures were 21 ± 0.3 °C and 9 ± 0.4 °C, respectively, it took 85 days to reach final shoot length. Mean solar radiation was 14 ± 0.7 MJ m^{-2} day^{-1}. Final leaf area increased with increasing PPFD. Shoots of shaded plants were shorter than shoots of plants in full sun. Leaf expansion rate was lower in the controls than in shaded plants, whereas there was no consistent effect of shading on the period of shoot extension. The modified logistic curves gave $r^2 > 0.93$ and $P < 0.001$.

Modeling

The curves developed from the models of Leverenz (1987) and Hanson et al. (1987) were similar to those of the exponen-

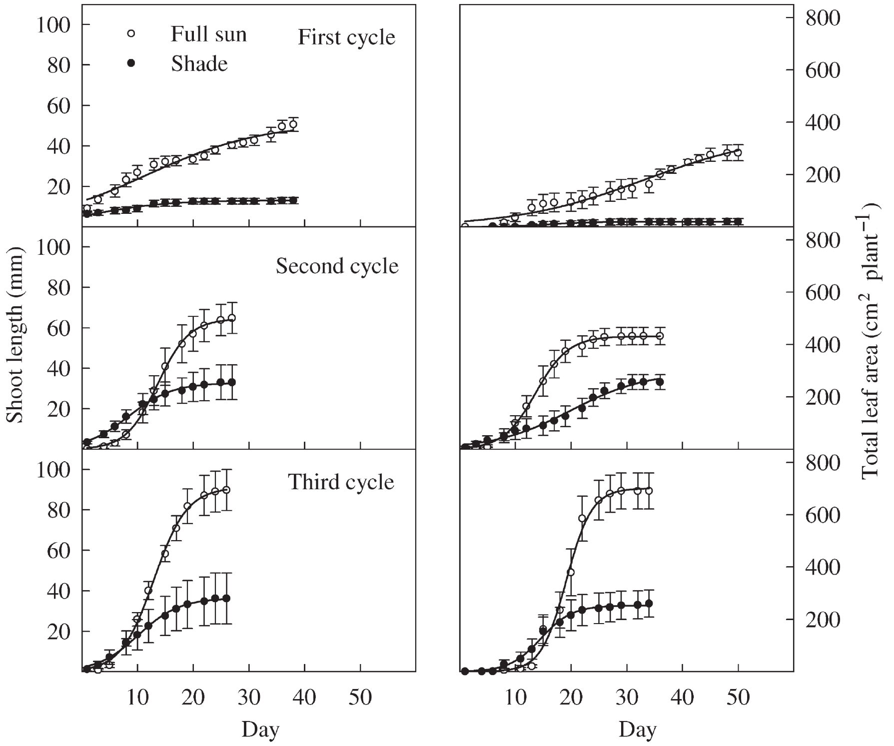

Figure 3. Effects of solar radiation on shoot growth and leaf area of potted lychee seedlings grown in a heated greenhouse over three flush cycles. Values are means (± SE) of eight plants. Regressions ($r^2 > 0.96$, $P < 0.001$) for shoot extension in full sun are: $S_1 = 52/(1 + \exp(-0.10(\text{day} - 11.7)))$, $S_2 = 65/(1 + \exp(-0.35(\text{day} - 13.6)))$ and $S_3 = 91/(1 + \exp(-0.33(\text{day} - 13.0)))$; and in shade $S_1 = 13/(1 + \exp(-0.15(\text{day} - 2.4)))$, $S_2 = 33/(1 + \exp(-0.25(\text{day} - 8.4)))$ and $S_3 = 36/(1 + \exp(-0.27(\text{day} - 10.2)))$; and for leaf area in full sun $L_1 = 361/(1 + \exp(-0.09(\text{day} - 33.2)))$, $L_2 = 431/(1 + \exp(-0.34(\text{day} - 13.7)))$ and $L_3 = 700/(1 + \exp(-0.44(\text{day} - 19.2)))$; and in shade $L_1 = 19/(1 + \exp(-0.27(\text{day} - 16.2)))$, $L_2 = 296/(1 + \exp(-0.15(\text{day} - 19.9)))$ and $L_3 = 253/(1 + \exp(-0.36(\text{day} - 14.6)))$ for the first, second and third cycles, respectively. Full sun at noon was equivalent to a PPFD of 1080 μmol m^{-2} s^{-1}.

tial model. Estimates of $A_{\max}$ for the "Kwai May Pink" trees and potted plants were similar for the three models, whereas the estimate for the "Salathiel" trees was higher in the Leverenz model (Table 2). Estimates of PPFD$_{\text{sat}}$ were higher with the Leverenz model in the trees, and lower in the potted plants compared with estimates from the exponential model. The Hanson model also gave lower values of PPFD$_{\text{sat}}$ in the "Kwai May Pink" trees and potted plants. The predicted photon irradiances associated with 50% of $A_{\max}$ (PPFD$_{50\%}$) were similar for the three models.

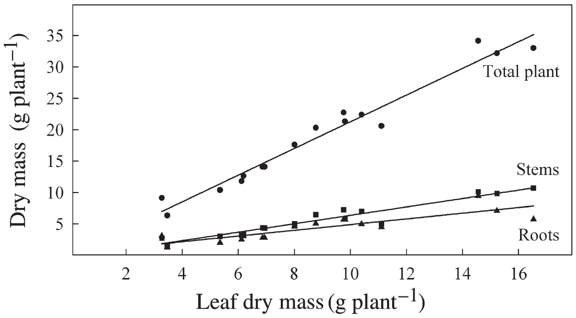

Figure 4. Relationship between leaf dry mass (W_L), and root (W_R), stem (W_S) and total plant dry mass (W_T) of lychee seedlings. Values are for potted seedlings grown in a heated greenhouse in full sun or shade ($n = 16$). Regressions are: $W_S = -0.34 + 0.67W_L$ ($r^2 = 0.92$, $P < 0.001$), $W_R = 0.36 + 0.45W_L$ ($r^2 = 0.73$, $P < 0.001$) and $W_T = 0.01 + 2.12W_L$ ($r^2 = 0.96$, $P < 0.001$).

Discussion

Solar irradiance had large effects on photosynthesis and growth of lychee trees and seedlings. Net CO_2 assimilation in individual leaves was saturated when irradiance reached half full sun, whereas maximum leaf expansion occurred at higher irradiances.

Leaf gas exchange of field-grown trees and potted plants

The gas exchange data for lychee are in agreement with the responses recorded for several temperate species (Leverenz 1987, Eamus and Murray 1991, Herrick and Thomas 1999), although not all these workers established when photosynthesis was saturated. Our ϕ values are close to those reported for tropical woody evergreens and other C_3 plants (Ehleringer and Björkman 1977, Wiebel et al. 1993, Whiley et al. 1999). Estimated ϕ was slightly lower in potted plants than in orchard trees, indicating a less efficient photosynthetic system in the potted plants. For lychee, the mean light compensation point, which is the PPFD required for photosynthesis to balance respiration, was calculated to be 23 μmol m^{-2} s^{-1}. However, because this estimate did not take into account the respiration in the rest of the tree or plant, the actual PPFD required to balance these respiratory loses will be higher than our estimate of the traditional light compensation point.

Potted plants had lower $A_{\max}$ than orchard trees. Photosynthesis of the potted plants was independent of PPFDs above 950 μmol m^{-2} s^{-1}, whereas CO_2 assimilation in the orchard trees increased up to at least half full sun. The restricted root systems of the plants grown in containers appeared to re-

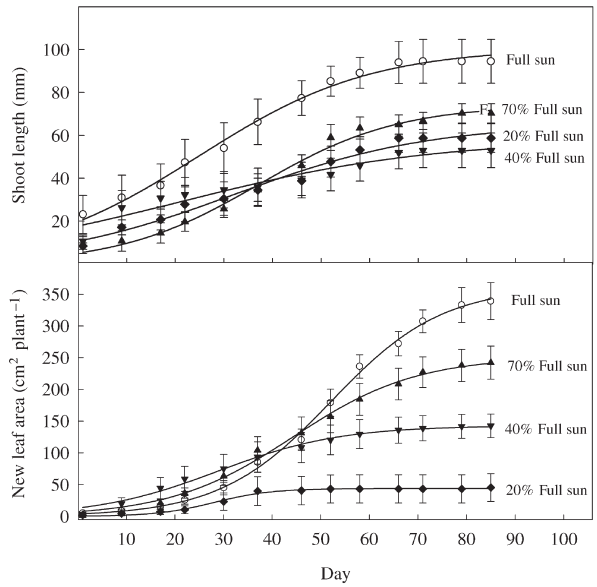

Figure 5. Effects of solar radiation on the growth of shoots and leaves of lychee plants raised outdoors in pots from June to September 1997. Values are means (± SE) of eight plants. Regressions ($r^2 > 0.93$, $P < 0.001$) for shoots are: $S_1 = 101/(1 + \exp(-0.06(\text{day} - 24.8)))$, $S_2 = 74/(1 + \exp(-0.07(\text{day} - 37.1)))$, $S_3 = 58/(1 + \exp(-0.04(\text{day} - 21.2)))$ and $S_4 = 65/(1 + \exp(-0.05(\text{day} - 32.4)))$; and for leaf area are: $L_1 = 362/(1 + \exp(-0.09(\text{day} - 52.1)))$, $L_2 = 251/1 + \exp(-0.08(\text{day} - 44.4)))$, $L_3 = 143/ (1 + \exp(-0.08(\text{day} - 28.9)))$ and $L_4 = 44/(1 + \exp(-0.17(\text{day} - 28.1)))$ for full sun, and 70, 40 and 20% of full sun, respectively. Full sun at noon was equivalent to a PPFD of 2000 μmol m^{-2} s^{-1}.

duce the capacity of the leaves to fix CO_2. Whiley et al. (1999) studied the effects of root restriction on gas exchange of avocado in subtropical Australia. Potted plants had lower A_{max} (5 versus 19 μmol CO_2 m^{-2} s^{-1}) and $PPFD_{sat}$ (586 versus 1270 μmol m^{-2} s^{-1}) than field trees. These authors suggested that root restriction in the pots led to accumulation of starch in the leaves and end-product inhibition of photosynthesis, although the root systems of potted plants might also be more sensitive to environmental stresses.

Table 2. Summary of gas exchange parameters of field-grown lychee trees and pot-grown lychee plants. Parameters A_{max}, $PPFD_{sat}$ and $PPFD_{50\%}$ were calculated from A versus PPFD (0–2200 μmol m^{-2} s^{-1}) based on three models: exponential, Leverenz (1987) and Hanson et al. (1987).

Parameters	Field-grown “Kwai May Pink” trees	Field-grown “Salathiel” trees	Pot-grown “Kwai May Pink” plants
A_{max} (μmol CO_2 m^{-2} s^{-1})			
Exponential model	12.6 ± 0.3	11.2 ± 0.2	6.3 ± 0.2
Leverenz model	13.0 ± 0.5	13.5 ± 0.9	6.1 ± 0.2
Hanson et al. model	12.3 ± 0.2	11.2 ± 0.2	6.2 ± 0.2
$PPFD_{sat}$ (μmol m^{-2} s^{-1})			
Exponential model	1214	1096	959
Leverenz model	1409	2822	675
Hanson et al. model	1062	1068	906
$PPFD_{50\%}$ (μmol m^{-2} s^{-1})			
Exponential model	367	329	289
Leverenz model	370	360	313
Hanson et al. model	346	324	288

Light can influence photosynthesis in plants in two main ways: by an effect on stomata and entry of CO_2 into the leaf and by an effect on the biochemistry of photosynthesis. If C_i falls with increasing PPFD, then A must exceed the rate of entry of CO_2 through the stomata. On the other hand, if C_i remains relatively constant, then there must be an equilibrium between CO_2 entry and fixation. Whiley et al. (1999) showed that, in avocado and mango, C_i decreased with increasing PPFD. We found that C_i decreased as PPFD increased, but there was no clear stomatal response. Even at low PPFDs, there was unrestricted CO_2 diffusion through the stomata, with the effects of light on CO_2 assimilation being mainly mediated by changes in leaf biochemistry.

Models of photosynthesis

We used an exponential model (Equation 1) to describe the relationship between A and PPFD, and compared it with the relationships developed by Leverenz (1987) (Equation 2) and Hanson et al. (1987) (Equation 3).

The values of ϕ calculated by least squares were slightly lower than those calculated by the regression of A versus PPFD from 0 to 100 μmol m^{-2} s^{-1} (Figure 1). The convexity coefficient (ρ) describes the transition between light-limited and light-saturated photosynthesis, with values close to one when the transition is abrupt. This case is more likely to occur in thin leaves where all chloroplasts are exposed to similar conditions (Riddoch et al. 1991). In thick leaves, the lower chloroplasts are relatively shaded so that they are not as readily light-saturated. It is not known if the difference in coefficient ρ between pot-grown (0.97) and field-grown lychees (0.84 for “Kwai May Pink” and 0.28 for “Salathiel”) was a result of differences in leaf thickness and chloroplast distribution.

Estimates of A_{max} for the “Kwai May Pink” trees and potted plants were similar to those predicted by the exponential model, whereas the estimate for the “Salathiel” trees was higher. The values of $PPFD_{sat}$ calculated from the regression were higher for field-grown plants and lower for potted plants than those calculated from the exponential curve. The value for the “Salathiel” trees was above full sun in the Leverenz model, indicating errors in the estimation of A at high PPFDs. It is noteworthy that Eamus and Murray (1991) and Herrick and Thomas (1999) did not use the Leverenz model to estimate A_{max} or $PPFD_{sat}$. The predicted solar irradiances associated with 50% of A_{max} were similar in the two models.

In the model of Hanson and co-workers, A is described in terms of A_{max}, R_d and the light compensation point. The estimates of A_{max} were similar to those derived from the exponential model. However, the values of R_d and compensation point were lower than those estimated in Figure 1, possibly because they were based on PPFDs above 100 μmol m^{-2} s^{-1}. The calculated values of PPFD_{sat} for the "Kwai May Pink" trees and potted plants were also slightly lower than those derived from the exponential model. In contrast, the predicted values of $\text{PPFD}_{50\%}$ were similar. The Hanson et al. model has been reported to describe A/PPFD relationships successfully in other North American conifer species (Bond et al. 1999).

Gas exchange in other tropical evergreen trees

Many of the earlier studies on photosynthesis in tropical trees were conducted on seedlings or small trees in pots in greenhouses, with irradiances well below full sun. Our maximum rates of CO_2 assimilation for lychee are similar or slightly lower than those reported for avocado and mango trees in subtropical Queensland (Whiley et al. 1999): the PPFD required to saturate photosynthesis was also slightly lower at 1100–1200 μmol m^{-2} s^{-1}. For mangosteen seedlings, Wiebel et al. (1993) determined an $A_{\max}$ of 4 μmol CO_2 m^{-2} s^{-1} and light saturation between 550 to 950 μmol m^{-2} s^{-1}.

Rainforest trees vary greatly in their adaptation to light (Thompson et al. 1988). Some species are shade intolerant and only establish when there are large gaps in the canopy, whereas others are shade tolerant or adaptable and can persist as shade-tolerant seedlings and regenerate in small canopy gaps. *Flindersia brayleyana* F. Muell. is an example of a species with a broad tolerance to sun and shade: seedlings can persist in the understory at 0.6% of full sun. Our results indicate that although lychee seedlings can persist in the forest understory, improved CO_2 fixation and growth are highly dependent on access to the high PPFDs prevailing in large canopy gaps.

Leaf expansion

The leaves expanded in a sigmoid pattern over 28 to 85 days depending on temperature and solar irradiance, with faster growth in spring and autumn than in winter. Leaves were much smaller in shade than in full sun. Shade leaves also tended to expand more quickly (lower m) compared with leaves growing in full sun. In contrast, PPFD did not affect leaf initiation, with similar numbers of leaves per flush in shaded and full-sun plants.

Although little is known about the effects of PPFD on leaf expansion in rainforest species, there have been several studies on herbaceous plants. Milthorpe and Newton (1963) and Newton (1963) found that the rate of leaf production in cucumber increased as radiation increased from 0.6 to 1.9 and 4.2 MJ m^{-2} day^{-1}. The higher value was equivalent to about half of daily radiation in England during spring and summer. Provided that nutrients were well-supplied, leaves expanded in a sigmoid fashion and were larger and thicker at high than at low irradiances (5.0 MJ m^{-2} day^{-1}) as a result of an increase in cell number before leaf unfolding. Under nutrient-poor conditions, maximum leaf area occurred at an irradiance of 1.9 MJ m^{-2} day^{-1}. Solar irradiance had no effect on cell size. In lychee, shaded plants had similar numbers of leaves as plants in full sun, but the leaves were smaller. In other subtropical species such as citrus and carambola (Syvertsen and Smith 1984, Marler et al. 1994), shading resulted in increased leaf area per plant.

Biomass production

Seedling biomass was increased by a factor of 1.7 in full sun compared with heavy shade, with both shoot and root growth reduced in shade. Shading also resulted in a reduction in the proportion of plant biomass allocated to roots. Chirachint and Turner (1988) reported that a 6-week shade treatment (PPFD = 725 μmol m^{-2} s^{-1}) had no effect on shoot growth of potted avocado plants, where full sun at noon was equivalent to a PPFD of 1350 μmol m^{-2} s^{-1}. It is possible that 6 weeks was too short a period for the shade treatment to have influenced biomass production, or that the PPFD during most of the day was above that required to saturate photosynthesis (Scholefield et al. 1980). Wiebel et al. (1994) found that mangosteen seedlings grown in 50 and 80% full sun were larger than those grown in 20% full sun, whereas seedlings grown in full sun were stunted. Avocado would be expected to be more responsive to PPFD than the shade-adapted mangosteen, because mangosteen is an understory rainforest tree, whereas avocado is a sub-story tree.

Thompson et al. (1992) compared the growth of seedlings of four rainforest species from northern Australia exposed to a 12-h photoperiod at a PPFD of 30 μmol m^{-2} s^{-1} equivalent to deep shade on the forest floor, 130 μmol m^{-2} s^{-1} equivalent to moderate shade at mid-canopy, or 532 μmol m^{-2} s^{-1} equivalent to high PPFDs on exposed crowns. Shade-tolerant *Argyrodendron trifoliolatum* F. Muell. exhibited a 2-fold increase in plant biomass from low to medium PPFD and a 5-fold increase at high PPFD, whereas *Toona australis* H., an early successional species, grew better in high PPFDs than in low PPFDs (20-fold increase in growth from low to medium and high PPFDs). *Flindersia brayleyana*, which has a broad tolerance to sun and shade, was intermediate in response to irradiance, with a 5-fold increase in plant biomass from low to medium and high PPFDs. Thus, lychee does not appear to be as sensitive to solar irradiance as early successional trees from north Queensland.

In shade, leaf growth of lychee continued at the expense of the roots, with higher shoot:root ratios in shaded seedlings compared with plants grown in full sun. Newton (1963) showed that roots and stems of cucumber were more sensitive to changes in radiation than leaves. It is possible that stems and roots are less able to import carbohydrates because they are further away from the site of photosynthesis in the leaves.

In summary, PPFD had large effects on photosynthesis and growth of lychee. Leaf photosynthesis was saturated at about half full sun, whereas maximum leaf expansion occurred at higher PPFDs. Lychee is a dominant species in the upper canopy of the rainforests in South-East Asia, but persists as a seedling on the forest floor. We conclude that much higher PPFDs are required for maximum growth and photosynthesis than for survival on the forest floor. Canopy management techniques that maximize light interception and distribution in orchard trees would therefore be expected to improve CO_2 fixation and fruit yields in lychee.

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