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Productivity of leaves of a tropical tree, *Theobroma cacao*, grown under shading, in relation to leaf age and light conditions within the canopy

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SUMMARY

The photosynthetic and respiratory activities of the leaves of a tropical tree, cacao, *Theobroma cacao* L., grown under shading, were determined in relation to leaf age and light conditions within the canopy, in order to gain a deeper insight into characteristics of the leaf population composing a canopy.

The specific leaf weight and leaf water content varied with the height of leaves from the ground and/or the irradiance. The net photosynthetic rate also varied markedly depending on leaf age and irradiance. The leaves in full or nearly full irradiance (< 70 % full daylight) attained the maximum rate c. 60 d after the leaves emerged, and the rate decreased to nearly zero at a leaf age of c. 270 d.

The nocturnal leaf respiratory activity was proportional to the photosynthetic activity during the day, but the proportional ratio was not constant throughout the survival period of leaves. Within the closed canopy, the upper leaves, which much higher ratios of respiratory to photosynthetic activity, under full or nearly full irradiance, tended to have much shorter mean longevities (c. 160 d) than the lower leaves under a lower irradiance (c. 310 d).

Key words: Canopy irradiance, leaf age, leaf photosynthesis and respiration, shading, *Theobroma cacao* (cacao).

INTRODUCTION

Only a few studies of the photosynthetic activity of leaves of tropical perennials have been carried out over the full life span of the leaves (Yamaguchi & Friend, 1979; Corley, 1983). The photosynthetic activity of *Coffea arabica* leaves decreased little after 150 d from expansion. (Yamaguchi & Friend, 1979), and the leaves of the oil palm, *Elaeis guineensis*, remained photosynthetically active for 21 months after their emergence, though with a decline in CO₂ uptake at saturating radiant energy after 11 months (Corley, 1983).

The net assimilation rate (NAR), as an indication of the productivity of leaves for a tropical broad-leaved evergreen, cacao (*Theobroma cacao* L.), has been determined for seedlings by means of growth analysis techniques by Goodall (1950), Murray (1953), Alvim

& Grangier (1966) and Alvim (1977). Their measurements indicate that cacao, like most tree crops, has a relatively low NAR, compared with herb crops (Alvim, 1977). The photosynthetic rates for individual leaves of cacao also have been measured by gas analysis techniques (Lemée, 1955; Baker & Hardwick, 1973, 1976; Hutcheon, 1976; Guers, 1985) and an improved half-leaf method (Miyaji, Silva & Alvim, 1985*a, b*). Lemée (1955) found that leaf photosynthetic rate increased with light intensity up to 25 % of full daylight, but further increases in light intensity up to 100 % full daylight exposure caused very little further increase in the photosynthetic rate. Miyaji *et al.* (1985*b*) reported that in seedlings, there were some genotypic differences in the photosynthetic rates of leaves relative to the irradiance received.

The relative shade tolerance of cacao has been shown by studies on light compensation points and by the responses of NAR (Alvim, 1977) and photosynthetic rates (Guers, 1985). Hence, for optimal

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growth, photosynthesis and yield of cacao trees, shading during cultivation is advantageous, and also helps to reduce the effects of unfavourable ecological factors, such as low soil fertility, wind damage, and excessive evapotranspiration leading to moisture deficiency (Cunningham & Burrige, 1960; Cunningham & Arnold, 1962; Ahenkorah, Akrofi & Adri, 1974; Hutcheon, 1976; Alvim, 1977; Alvim, Alvim & Leite, 1978; Miyaji, Silva & Alvim, 1997). However, excessive shading not only decreases the yield because of lower photosynthetic production (Alvim, 1977; Ng, 1982) but also leads to an increase in the incidence of black-pod disease caused by *Phytophthora palmivora* (Alvim, 1977). Therefore, in commercial plantation practice, it is critical to understand in detail the potential productivity of canopy leaves of cacao trees under various shading levels, relative to pod-set and yield (Hurd & Cunningham, 1961; Asomaning, Kwaka & Hutcheon, 1971; Alvim, 1977).

However, very few studies on potential leaf productivity, based on the rates of photosynthesis and respiration, of leaves within the cacao canopy related to leaf age throughout the lifespan of the leaves and the irradiance received, have been carried out with adult trees under levels of shading used in commercial plantations (see 'Materials and Methods' for details). Miyaji *et al.* (1997) determined the longevity of leaves, a basic factor in productivity, of a cacao tree population growing under shading in relation to their position within the canopy and the time of emergence. Their results showed that the longevity of leaves decreased greatly with increasing height above ground level, and/or the irradiance received, and the main leaf mortality factor was 'physiological leaf-fall', which followed normal senescent processes in leaves showing a low level of photosynthesis.

The primary objective of the present investigation was to gain a better understanding of the productivity of leaves within the canopies of tropical adult trees under various shade regimes, with the goal of relating the productivity to leaf longevity and mortality. Data are given on the activities of photosynthesis and respiration of leaves in adult field trees of cacao, under commercial levels of shading and relative to leaf age and light conditions within the canopy.

MATERIALS AND METHODS

Material and study site

The materials and methods for the present research have been previously described by Miyaji *et al.* (1997). A cv. of cacao (*Theobroma cacao* L.), Catongo, was used for the research. The investigation was made at the 7-yr-old plantation of the Cacao Research Center (Centro de Pesquisas do

Cacau; latitude 14° 47' S, longitude 39° 16' W), near the port of Ilhéus in Bahia State, Brazil. The research site, which is located in the tropical rain forest region of Bahia State, has a mean annual temperature of 23.5 °C and an annual total rainfall of *c.* 1700 mm, but with variations in rainfall pattern from year to year (Alvim & Alvim, 1978).

The closed canopy of cacao trees is 3–4 m high, and planted according to local farming technique in a 3 × 3 m pattern; the leaf area index (LAI) was *c.* 3.9, with an extinction coefficient of *c.* 0.61 (Miyaji *et al.*, 1997). The closed cacao canopy was shaded, somewhat irregularly, by *Erythrina fusca* and *Erythrina poeppigiano* 10–20 m tall, planted 24 m apart. In the experimental stand, the relative light intensity just above the cacao canopy ranged between 30 and 100% of full daylight, and 4–10% at ground level (Miyaji *et al.*, 1997).

Specific leaf weight and leaf water content determinations

The stratified clip technique (Monsi & Saeki, 1953) was used to obtain the canopy profile of leaf characteristics in the cacao tree population. Clippings were made in 40%-shaded and in unshaded areas, as previously reported by Miyaji *et al.* (1997), from 1 to 3 October 1984, when the leaf biomass of shade trees was at its maximum. The trees were sampled in an area of 3 × 6 m, and two trees were sampled in each area.

All leaves (leaf blades) of each of the sampled trees were clipped every 30 cm above ground level. The area, and fresh and dry weights of all the leaves clipped in each 30-cm layer above ground level were determined. The area (one side) of each leaf was measured with an automatic area meter (Hayashi Denko Co., Ltd, Japan), and d. wt was obtained by drying to a constant weight at 80 °C in a ventilated oven. The weight of leaf water was then obtained from the difference between the fresh and dry weights of leaves. Specific leaf weight (leaf d. wt per unit leaf area, mg cm⁻²) and the leaf water content (the ratio of leaf water weight to leaf f. wt, %) were computed from primary data for each layer of leaves every 30 cm above ground level.

Just before the clipping, the solar irradiance (kW m⁻²) within the canopies of both areas was measured in a horizontal plane, every 30 cm above ground level, using three tube solarimeters (970 mm long, 26 mm diameter; Delta-T Devices Ltd, UK), attached in a single row to one side of a bar 3 m long. These measurements were carried out in diffused light (not in direct solar radiation) at about noon. The irradiance was then calculated in terms relative to full daylight, which was measured outside the canopy in $\mu\text{mol m}^{-2} \text{s}^{-1}$ with a PAR (photosynthetically active radiation) Quantum Meter (Lambda Inst. Corp., USA) at the same time and converted

into kW m^{-2} using a calibrated curve relating kW m^{-2} to daylight $\mu\text{mol m}^{-2} \text{s}^{-1}$. The calibrated curve was previously produced from the output values observed at the same time for both the solarimeters and quantum meter under a range of intensities of daylight.

Photosynthetic and respiratory activities

Photosynthetic and respiratory processes were calculated by means of the improved half-leaf method (Nomoto & Saeki, 1969; Miyaji & Tagawa, 1979; Miyaji *et al.*, 1985*a*). Their rates were determined for the healthy leaves (without infection and injury) from 500 shoots selected randomly at different levels of shading from the 10 randomly chosen trees of cacao in the study area presented previously by Miyaji *et al.* (1997). A heated mosquito-repellent 'increase' coil was used in place of a steam-jet to stop the translocation from the leaf of assimilates in the phloem of the leaf stalk (Miyaji, 1984). Beforehand, a cut *c.* 1 mm deep was made in a ring around the leaf stalk, and the cut zone was then touched by the heated mosquito-coil. Aluminium foil wrapped around the softened stalk provided support.

A leaf was punched (to release leaf discs 1.74 cm diameter) twice each to determine net photosynthetic rate (P'_n , $\text{mg (d. wt) dm}^{-2}$ (leaf) h^{-1}) and daily surplus production (P'_s , $\text{mg (d. wt) dm}^{-2}$ (leaf) d^{-1}). For P'_n , the leaf was punched between 2 and 4 h after sunrise, and then about 2 h before sunset on the same day. For P'_s , the first time was between 4 and 5 h after sunrise (on the same day as the P'_n determinations), and the second about 5 h after sunrise on the following day. Leaf discs (one disc area: $2.36 \pm 0.036 \text{ cm}^2$; total (one punching) area: $80\text{--}100 \text{ cm}^2$) were put in a weighing bottle to which a drop of 80% ethyl alcohol was added to reduce enzyme activity, and were dried quickly at 80°C to constant weight, then weighed. Discs were taken from two to four leaves of the same age on a shoot at the same sampling time. Rates of dry matter production, i.e. P'_n and P'_s , were calculated from the differences in dry weights of the leaf discs between the first and second punchings.

The average height of the punched leaf surfaces on the shoot was recorded, and the irradiance at the average height on the punched leaf surfaces was measured at about noon just after the second punching for the P'_s , using a PAR Quantum Meter (as described above). The irradiation was then calculated relative to the full daylight measured outside the canopy at the same time.

The rate of nocturnal leaf respiration (R'_L , $\text{mg (d. wt) dm}^{-2}$ (leaf) h^{-1}) was calculated as:

$$R'_L = ((N-1)P'_n - P'_s)/(24-N)$$

where N is the duration of sunshine (day) as h, $N-1$ is the duration in which P'_n will become a positive value, and $24-N$ are the actual hours of night. The

rates (P'_n , P'_s and R'_L) were multiplied by the $[\text{6CO}_2]/[\text{C}_6\text{H}_{10}\text{O}_5]$ factor, $1.00/0.61$, to obtain CO_2 flux rates.

These measurements were carried out every 7–14 d from October 1983 until August 1984. All samplings were made on clear days (with full daylight).

Meteorological data were obtained from a Meteorological Station of the Cacao Research Center located about 100 m from the study site.

RESULTS AND DISCUSSION

Irradiance, specific leaf weight and leaf water content within the canopy

Vertical distributions of irradiance, specific leaf weight (SLW) and leaf water content (LWC) within the canopies of 40%-shaded and unshaded areas are presented in Figure 1. Each point in Figure 1*a* represents the mean value of two measurements at 30-cm intervals above ground level, and in Figure 1*b, c* indicates the value for all the leaves clipped in each 30 cm layer above ground level. The irradiance is plotted in relative terms of full daylight.

In the lower canopy layer (60–90 cm above the ground, relative irradiance of 3.9–4.8% in 40%-shading and 11.3–11.7% in unshaded areas) the typical values of SLW for 40%-shaded and unshaded areas were 5.1 and 7.0 mg cm^{-2} , respectively, whereas in the uppermost layer (some 30 cm below the canopy surface) the value was *c.* 9.8 mg cm^{-2} for both areas.

These results show that SLW, which correlates closely with leaf thickness, increases with irradiance. This information on differences in specific leaf weight within the canopy, which is similar to that already reported for a few other forest types (e.g. Nishioka *et al.*, 1978; Yoda, 1983), might be closely related to the photosynthetic and respiratory activities of the cacao leaves (Balasimha, Subramonian & Subbaiah, 1985).

In the middle and upper layers (more than 150 cm above ground), LWC was fairly constant, at *c.* 51–55%. In the lowest layer (60–90 cm), however, the value was 70% for the 40%-shaded areas and 55% for the unshaded areas. This result clearly shows that in the lower canopy (less than 150 cm above ground) in 40%-shading LWC varies with height from the ground, and/or positional irradiance, increasing as irradiance decreases. This also implies that cacao trees with overhead shade exhibit a high leaf water potential in the lower canopy (Alvim, Machado & Vello, 1974).

Rate of net photosynthesis related to leaf age and irradiance within the canopy

To convey comprehensive information on the relationships between canopy irradiance, leaf age and

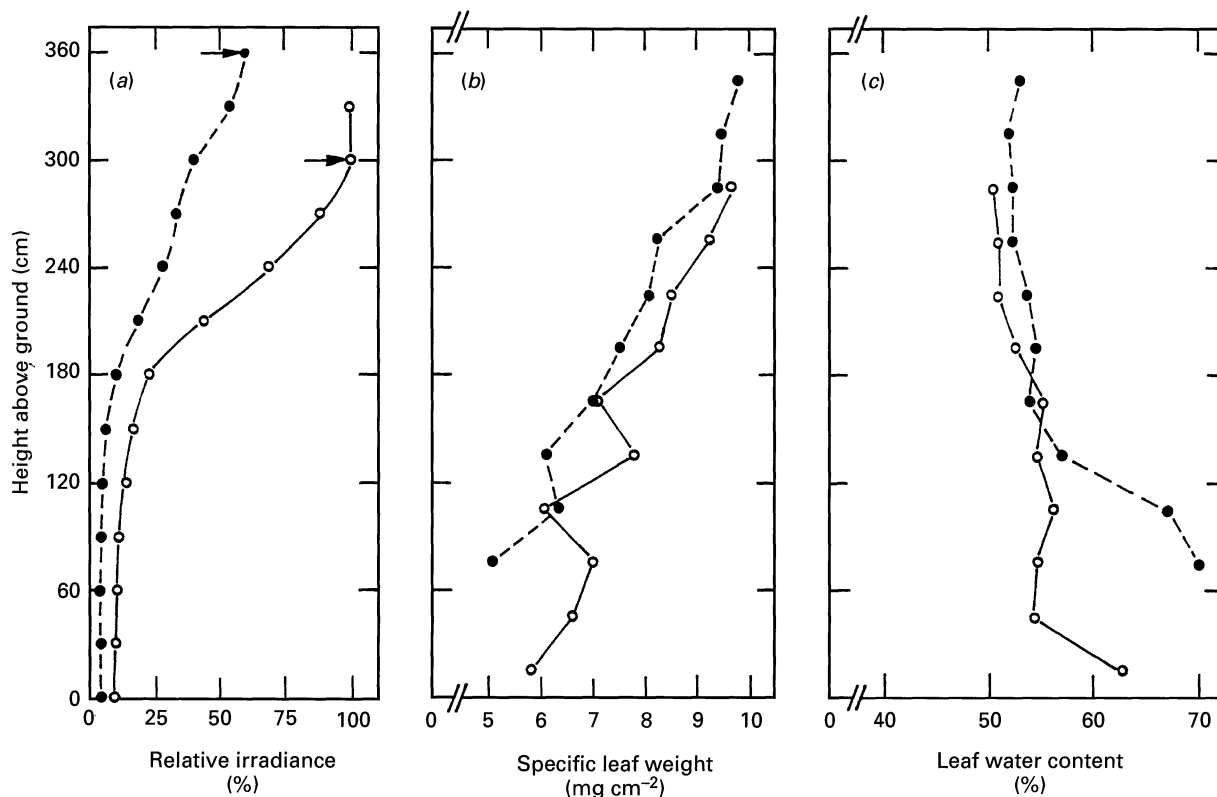


Figure 1. Vertical distributions of relative irradiance (a) specific leaf weight (b) and leaf water content (c), determined using all the leaves clipped every 30 cm above ground level, within the canopies in 40% -shaded (●, ----) and unshaded (○, —) areas. The arrows in the left figure (a) indicate the top surface of the canopies. Each value of the irradiance is the mean of two measurements. Relative irradiance of 100% represents full daylight.

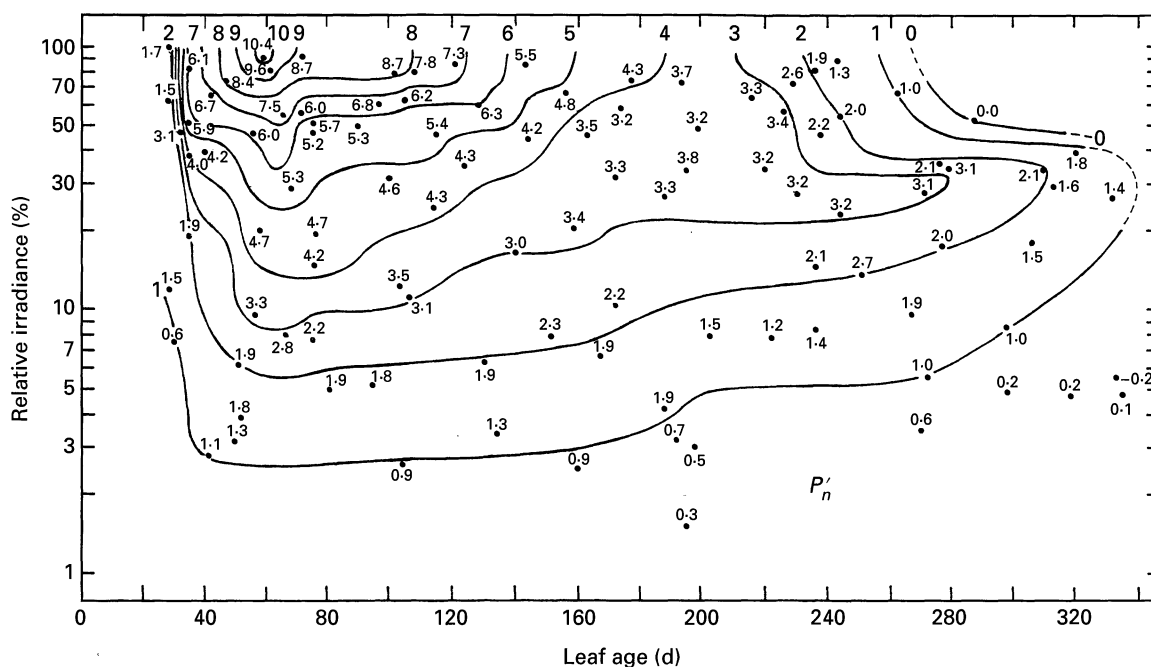


Figure 2. Isopleths of net photosynthetic rate (P'_n , mg d. wt dm⁻² leaf h⁻¹) in relation to leaf age and relative irradiance (log scale) incident on the measured leaves within the canopy. A number with a dot shows the mean value of P'_n for two or three measurements. Relative irradiance of 100% represents full daylight incident on the measured leaves.

productivity of canopy leaves under commercial levels of shading, the observed values of net photosynthetic rate (P'_n , mg (d. wt) dm⁻² (leaf) h⁻¹)

are shown as isopleths in Figure 2 in relation to the age of leaves and the irradiance of the measured leaves within the canopy. The irradiance is plotted

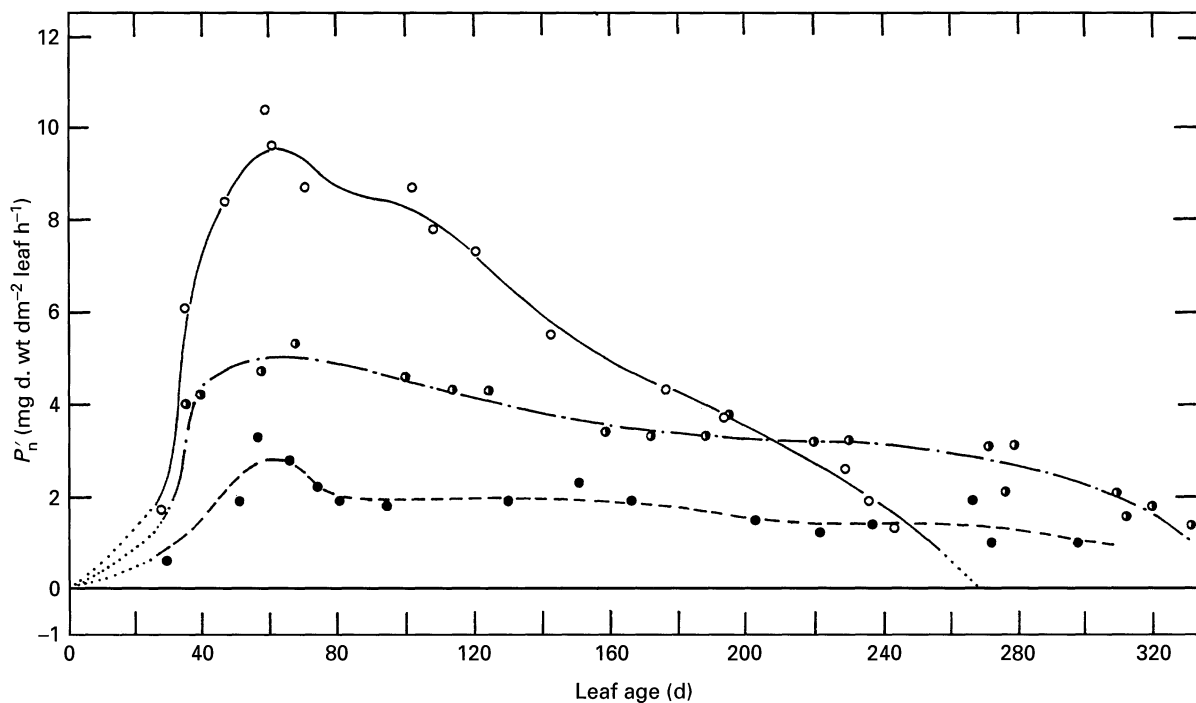


Figure 3. Time-trends of net photosynthetic rate (P'_n) for shade (●, ----), semi-shade (◐, - · - ·) and sun (○, —) leaves within the canopy. Irradiances on shade, semi-shade and sun leaves are at 5–10, 20–40 and 70–100% of full daylight, respectively. Each point plotted represents the mean value of two or three measurements.

relative to full daylight on a log scale, because of exponential attenuations of irradiance within the cacao canopies (Miyaji *et al.*, 1997).

The P'_n under full or nearly full daylight (relative irradiance 90–100%) showed a maximum rate of $10.4 \text{ mg dm}^{-2} \text{ h}^{-1}$ (corresponding to a net uptake of *c.* $17.0 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) at 59 d after leaf emergence. The rate then fell to *c.* $5.0 \text{ mg dm}^{-2} \text{ h}^{-1}$ at a leaf age of 160 d. Under low light conditions (2–3% relative irradiance), however, the leaves attained a much lower P'_n , of *c.* $1.0 \text{ mg dm}^{-2} \text{ h}^{-1}$ between leaf ages of 40–180 d.

This situation is more distinctly presented in Figure 3, which shows the time trends of P'_n for three different leaf types, shade, semi-shade and sun leaves, on which incident irradiances are 5–10, 20–40, and 70–100% of full daylight, respectively.

At a leaf age of *c.* 60 d, when the leaves attained a maximum P'_n for each of the three leaf types, the P'_n was *c.* 10, 5 and $3 \text{ mg dm}^{-2} \text{ h}^{-1}$ for sun, semi-shade and shade leaves, respectively. Afterwards, the P'_n value for sun leaves decreased rapidly to almost zero at *c.* 270 d, whereas the value for shade leaves declined much more gradually, being maintained between 2 and $1 \text{ mg dm}^{-2} \text{ h}^{-1}$ for 80–300 d after leaf emergence. According to the survivorship curves and mean longevity for cacao leaves reported previously (Miyaji *et al.*, 1997), it seems that for the shade leaves, under lower irradiance throughout their lifespan, the lower P'_n will continue to a leaf age of *c.* 310 d (corresponding to the mean longevity).

In the cultivated populations of soybean (*Glycine max*) and kidney bean (*Phaseolus vulgaris*) plants with continuous leaf production (in cacao it is discontinuous), the P'_n for leaves in the upper layer under full daylight tended to decline gradually because of leaf senescence from *c.* 20 d after leaf emergence. For leaves in the lower layer the decrease was very rapid, from *c.* 10 d, owing to both leaf senescence and rapid development of shading ('irradiation deficiency'), caused by the rapid development of foliage above (Miyaji, 1984, 1986). These results differ considerably from those for canopy leaves of cacao as described above. It appears that for trees and herbs with broad leaves the age-dependency of photosynthetic activity depends not only on leaf senescence but also on light conditions on the leaves, caused by differences in foliage development and/or in pattern of leaf production within the canopy.

When studying the influence of irradiance on the net photosynthetic rate of individual cacao leaves by a gas analysis technique, Lemée (1955) found that the rate increased rapidly from 7 to $22 \text{ mg CO}_2 \text{ dm}^{-2} \text{ (leaf) d}^{-1}$ when the light intensity increased from 2 to 25% of full daylight, but then tended to level off at *c.* $27 \text{ mg CO}_2 \text{ dm}^{-2} \text{ d}^{-1}$ in irradiances up to 100% of full daylight. Hutcheon (1976) showed that the net photosynthetic rate for cacao leaves varied with the type of tree growth (i.e. degree of tree vigour), and ranged from *c.* $3\text{--}7 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ at light-saturation point. These maximum values of net photosynthetic rate are much lower than those found here

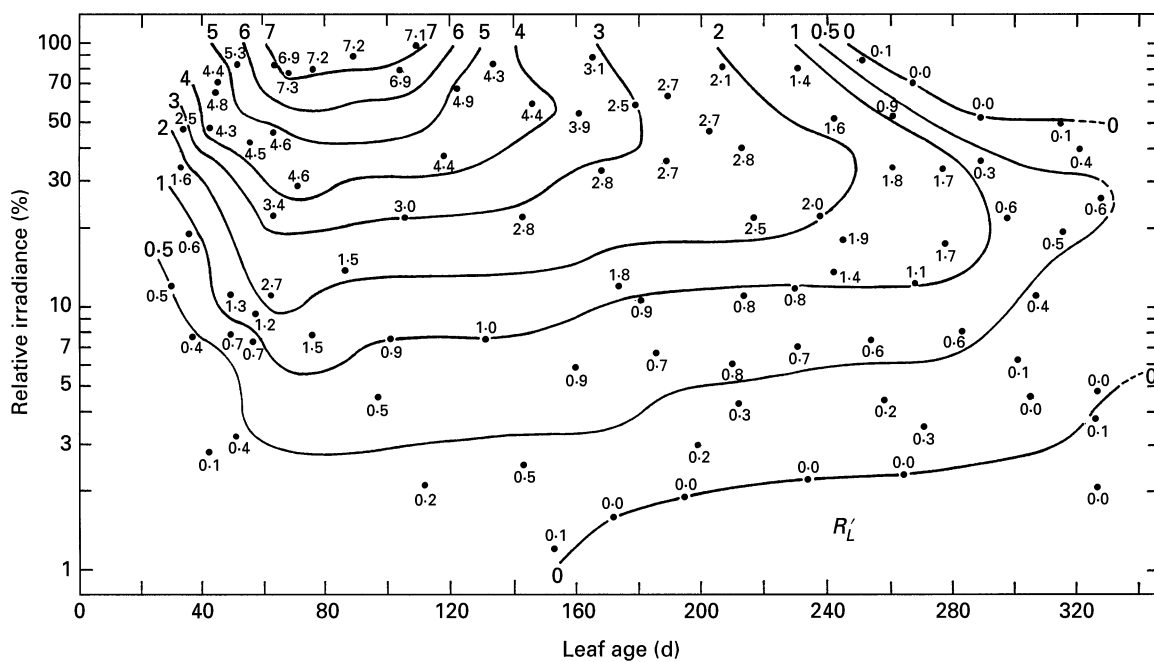


Figure 4. Isopleths of nocturnal leaf respiration rate (R'_L , mg d. wt dm^{-2} leaf h^{-1}) as related to leaf age and relative irradiance (log scale) during daylight, of the measured leaves within the canopy. A number with a dot shows the mean value of R'_L for two or three measurements. Relative irradiance of 100% represents full daylight incident on the measured leaves.

(Fig. 2) and lower than those (9–15 $\text{mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$ at a light saturation point) for *Shorea pauciflora* and *Dipterocarpus* spp. as native trees (not crops) in the upper part of a lowland rain forest in Peninsular Malaysia (Koyama, 1981). These lower photosynthetic rates recorded by Hutcheon (1976) might be due to differences in leaf type caused by the irradiance received by the leaves (as described below) and/or the age of leaves sampled.

Nocturnal leaf respiration rate related to leaf age and canopy light conditions during daylight

Figure 4 shows the observed rates of nocturnal leaf respiration (R'_L , mg (d. wt) dm^{-2} (leaf) h^{-1}), together with the isopleths, related to leaf age and the relative irradiance in the day on the measured leaves within the canopy.

The value of R'_L for the leaves receiving full or nearly full daylight (relative irradiance of > 90%) showed a maximum of $c. 7 \text{ mg dm}^{-2} \text{ h}^{-1}$ (corresponding to a net CO_2 efflux of $c. 11.4 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) between leaf ages of 60–110 d. The rate then decreased to $c. 2 \text{ mg dm}^{-2} \text{ h}^{-1}$ at 210 d. For the leaves existing in very dark conditions (relative irradiance of 2–3%) during the day, the R'_L value was $c. 0.5 \text{ mg dm}^{-2} \text{ h}^{-1}$ at 60–110 d after the leaves emerged. Afterwards, the rate decreased very gradually to nearly zero at a leaf age of 310 d and thereafter. The high rate of nocturnal respiration of cacao leaves receiving intense irradiation would be closely related to the relatively low NAR (5–20 $\text{mg dm}^{-2} \text{ d}^{-1}$), determined by Goodall (1950), Murray

(1953) and Alvim (1977), through more consumption of assimilates produced during the day.

Time trends of R'_L for the three different leaf types are shown in Figure 5. Through considering the results of the time trends of R'_L , together with P'_n (Fig. 3), two interesting observations emerge concerning the productivity of leaves within the cacao canopy under shading. The first is that for each of the leaf types, pattern of change over time of the rate of nocturnal leaf respiration was extremely similar to the change in net photosynthetic rate, i.e., that the activity of nocturnal leaf respiration was proportional to photosynthetic activity during the day. In a population of kidney bean plants, a similar phenomenon was seen for leaves within the canopy, and moreover, the daily rate of total canopy leaf respiration was almost proportional to that of the canopy gross photosynthesis for the various leaf area indices of the canopy (Miyaji, 1986). McCree & Troughton (1966) also found that when white clover (*Trifolium repens*) plants were grown in controlled growth cabinets, rates of respiration quickly (within $c. 24 \text{ h}$) changed relative to incident light levels, and that the final respiration rate was proportional to photosynthetic rate over a wide range of light levels.

The other observation is that the changes over time for rates of both net photosynthesis and nocturnal leaf respiration were very different for the sun (upper canopy) and shade (lower canopy) leaves. This implies a distinction of leaf type concerning productivity relative to leaf age caused by the differences in the irradiance received by the leaves within the canopy.

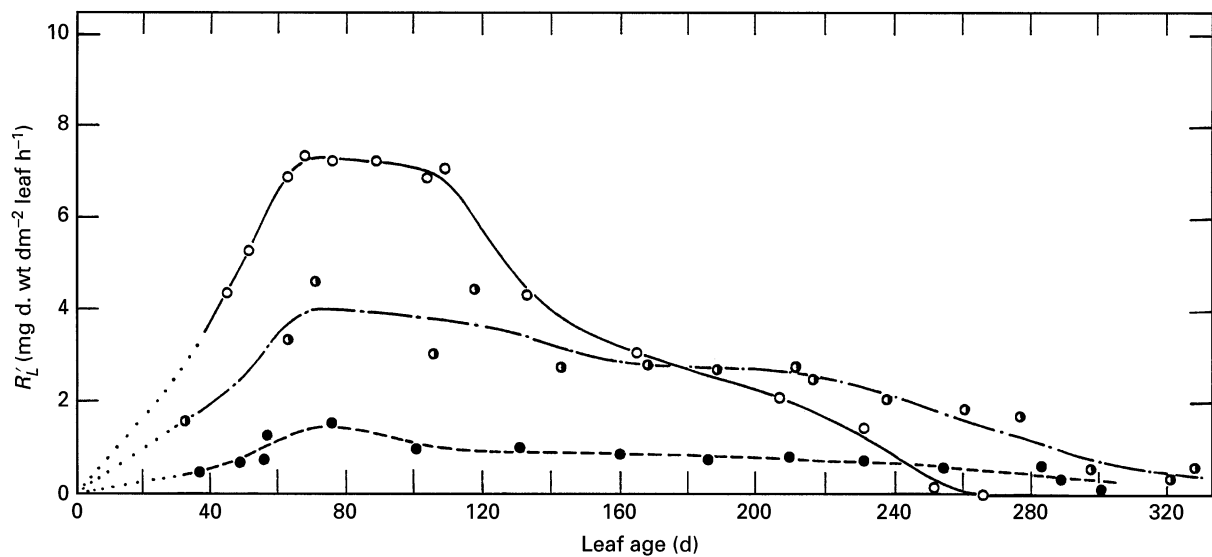


Figure 5. Time-trends of nocturnal leaf respiration rate (R'_L) for shade (●, ----), semi-shade (◐, - · - ·) and sun (○, —) leaves within the canopy. Irradiances on shade, semi-shade and sun leaves are at 5–10, 20–40 and 70–100% of full daylight, respectively. Each point plotted represents the mean value of two or three measurements.

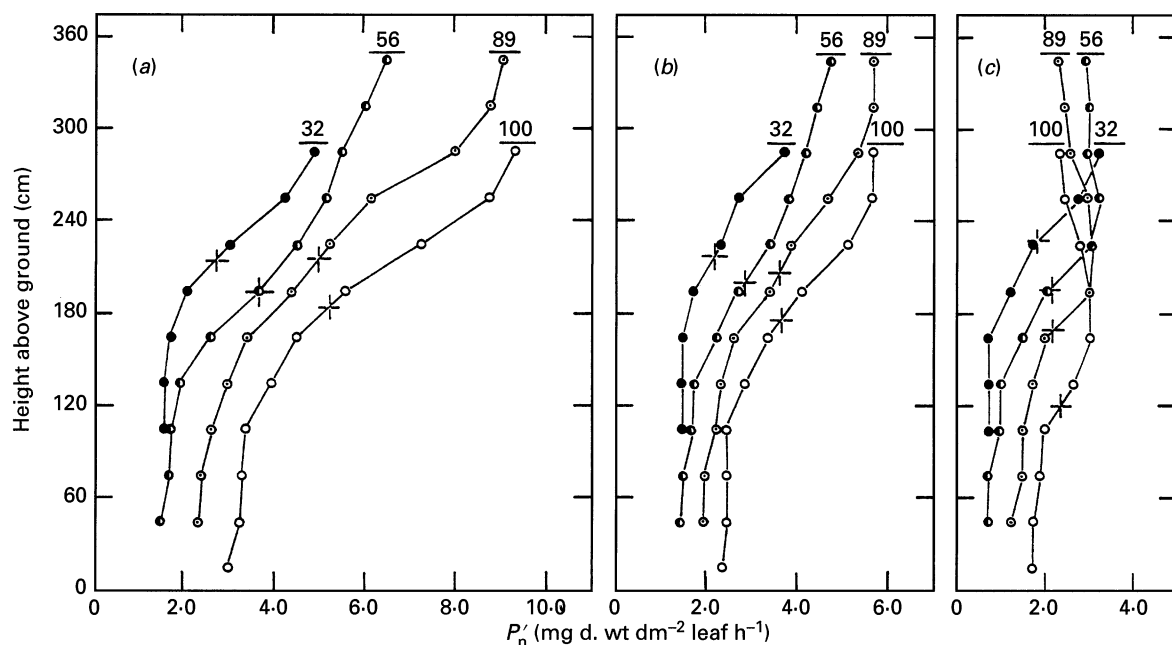


Figure 6. Net photosynthetic rates (P'_n) of leaves at different levels within the canopies under four shade conditions: 32 (●), 56 (◐), 89 (◑) and 100% (○) daylight just above the canopy. (a) 50–80 d old. (b) 130–160 d old. (c) 210–240 d old. A number and cross in each plot shows the relative irradiance just above the canopy as a percentage for full daylight and a mean value of P'_n for leaves under the given light conditions, respectively.

Rates of net photosynthesis and nocturnal leaf respiration of leaves at different levels within the canopy

Ng (1982), using a simulation model, but without considering leaf-age effects, reported that the LAI of the overhead shade had considerable effect on the canopy photosynthesis, the rate declining by 25 and 50% with a shade canopy LAI of 0.5 and 1.0, respectively.

Figures 6 and 7 indicate the vertical distributions of the P'_n and R'_L values, respectively, for leaves at different levels in the canopy and of three different leaf ages (50–80, 130–160 and 210–240 d) under four different shading conditions: 32, 56, 89 and 100% daylight just above the canopy, as previously cited by Miyaji *et al.* (1997). The P'_n and R'_L values were calculated from the graphs of the photosynthetic and respiration rate isopleths (Figs 2, 4), together with measurements of irradiance attenuation within the

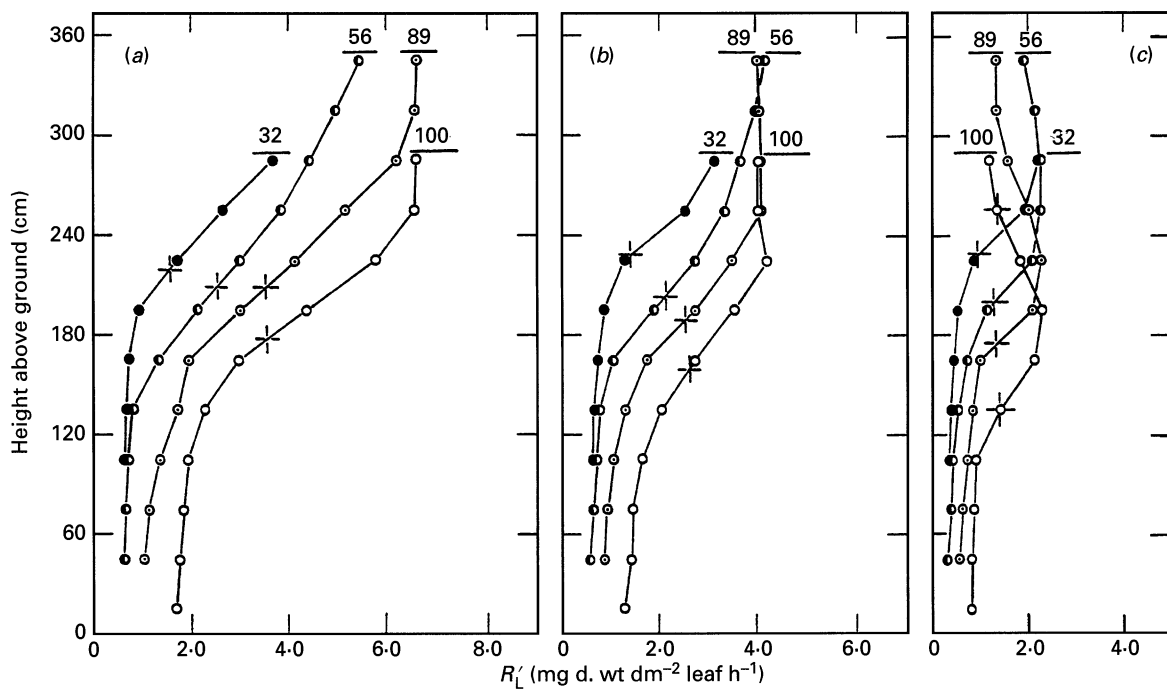


Figure 7. Nocturnal leaf respiration rates (R'_L) for leaves at different levels within the canopies under four different shading conditions: 32 (●), 56 (●), 89 (○) and 100% (○) daylight just above the canopy. (a) 50–80 d old. (b) 130–160 d old. (c) 210–240 d old. A number and cross in each plot shows the relative irradiance just above the canopy as a percentage for full daylight and a mean value of R'_L for leaves under the given light conditions, respectively.

canopies under the four levels of shade (Miyaji *et al.*, 1997).

The values on both graphs further verified that, within the cacao canopies and with different shade levels, rates of R'_L were proportional to P'_n rates during the day, regardless of the age of leaves. For both the P'_n and R'_L the rates of young leaves 50–80 d) (Figs 6a, 7a) within the unshaded canopy varied greatly depending on position (height above ground level) within the canopy, and/or irradiance. The P'_n and R'_L values for older leaves (210–240 d) (Figs 6c, 7c) were within a narrow range, irrespective of height above ground within the canopy and the degree of shade cast by shade trees. The P'_n and R'_L values for younger leaves in the lower canopy were much lower in heavy shade, but, conversely, for the older leaves in the upper canopy, rates were lower in full daylight.

These findings clearly show that the photosynthetic and respiratory activities of leaves within the cacao canopy, grown under commercial levels of shading, are greatly dominated not only by the canopy shading conditions but also by the ages of leaves.

Ratio of nocturnal respiratory rate to gross photosynthetic rate of leaves

For the sun and shade leaves, the gross photosynthetic rate (P'_g , mg (d. wt) dm^{-2} (leaf) h^{-1}) was calculated as $P'_n + R'_L$, assuming that the rates of daytime and nocturnal leaf respiration are equiva-

lent. Time trends of the R'_L/P'_g ratios for the sun and shade leaves, which were estimated from the time trends of P'_n (Fig. 3) and R'_L (Fig. 5), are shown in Figure 8.

At a leaf age of *c.* 80 d, when the R'_L values were at the maximum (cf. Fig. 5), the ratio of R'_L/P'_g was also at a value of 46% for sun leaves and 41% for shade leaves, then decreased to *c.* 40 and 30%, respectively, and remained at those levels for *c.* 220 d.

These results indicate that although the nocturnal leaf respiration is proportional to the photosynthesis in the daytime, the proportional ratio is not constant throughout the life span of leaves. Moreover, it shows that the R'_L/P'_g ratio for sun leaves was larger than that for shade leaves between leaf ages of 30–240 d. This suggests that for mature leaves in the uppermost canopy the much greater leaf respiration activity markedly reduces the dry matter (carbohydrate) produced by the much greater photosynthetic activity, so that the uppermost leaves have relatively low values of daily surplus production.

The life span of cacao leaves varied greatly depending upon position within the canopy and/or the irradiance received by leaves. The mean longevity for the lower leaves (0–150 cm high) under 5–20% daylight was about twice that for the upper leaves (> 220 cm high) under more than 60% daylight (Miyaji *et al.*, 1997). The present data, on the ratios of respiratory to photosynthetic activities of leaves, might give a clue to why leaves in the upper foliage had a much shorter than life span than the lower. It seems possible that for the mature leaves in

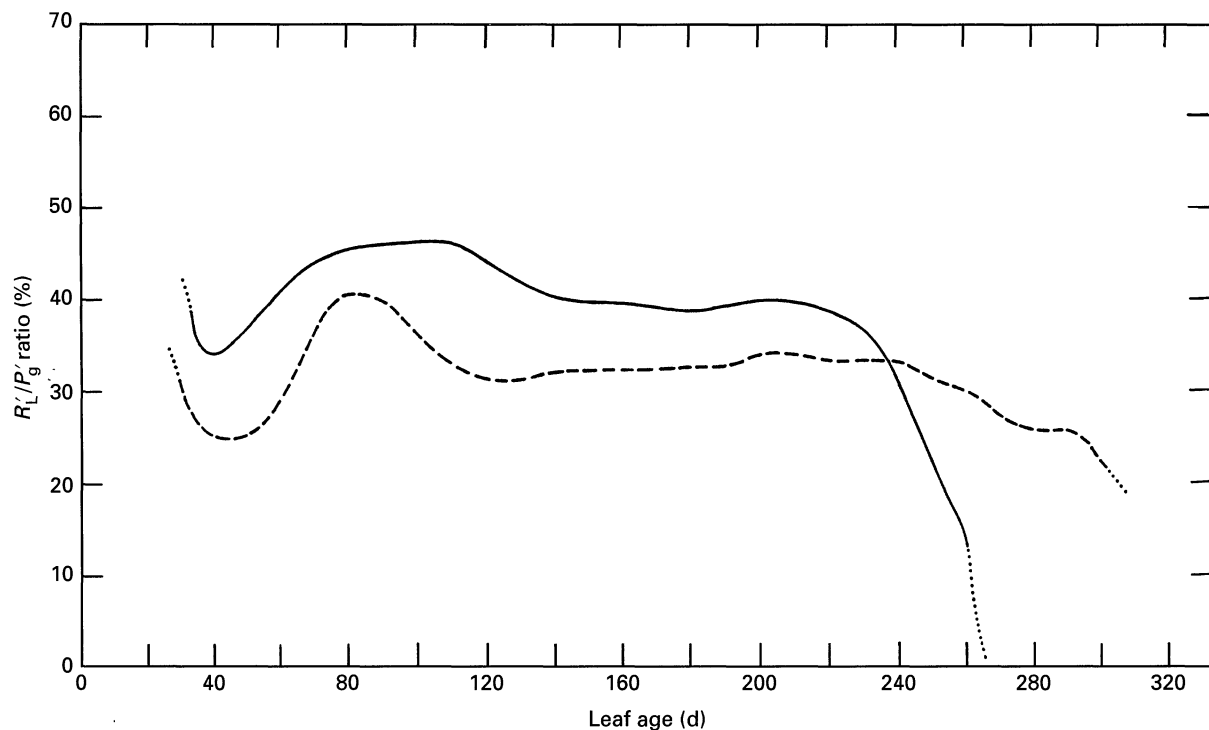


Figure 8. Time-trends of the ratio of leaf respiration rate (R'_L) to gross photosynthetic rate (P'_g), R'_L/P'_g ratio, estimated for shade (----) and sun (—) leaves within the canopy. Irradiances on shade and sun leaves are *c.* 5–10 and 70–100 % of full daylight, respectively. The P'_g was defined as $P'_n + R'_L$, assuming that the daytime and nocturnal leaf respiration rates are equivalent. The time-trends of the R'_L/P'_g ratio were estimated from the time-trends of P'_n (Fig. 3) and R'_L (Fig. 5) for the leaves concerned.

the upper layer under higher irradiance (full or nearly full daylight), the much greater respiratory activity (cf. Figs 5, 8) relative to photosynthesis (cf. Fig. 3) results in the acceleration of leaf senescence and much shorter longevity of the leaves than of the lower foliage under lower irradiance. The earlier senescence and death of the upper leaves might possibly be induced by greater consumption of carbohydrate in individual leaves and other physiological responses caused by the much greater respiratory activity, in proportion to photosynthetic activity. However, further research is needed to clarify this point. A similar situation was observed for the upper leaves within the kidney bean canopies, i.e., the upper foliage had a much higher rate of nocturnal respiration and a shorter mean longevity than the leaves of the middle canopy level (Miyaji, 1986).

Other relationships between productivity and longevity of cacao leaves will be detailed in a later paper, using the new life-table approach (Morisita, 1973; Miyaji, 1984, 1986), in which the leaf demography study was closely combined with data on productivity, for the leaf population of the adult trees.

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