

Is shade important in rubber based cropping systems? Part 2. Photosynthetic performance of rubber and banana under natural shade

A M W K Senevirathna*, C M Stirling**, V H L Rodrigo*,
P K W Karunathilake* and P D Pathirana*

Received 13 August 2002; Accepted 19 September 2002

Abstract

Shade effects on photosynthetic performance of rubber and banana were studied under natural shade established in an existing mature rubber plantation. Four treatments were imposed consisting of an unshaded control and three levels of shade with a 33, 55 and 77% reduction in incoming radiation. Chlorophyll fluorescence revealed no evidence of sustained photoinhibitory damage to photosynthesis under high light conditions in either banana or rubber. Short-term dynamic photoinhibition resulted in a reduction in photosynthetic efficiency during the central hours of the day in unshaded plants of both crops. Dynamic photoinhibition of both rubber and banana decreased with increasing shade, with the greatest depression in F_v/F_m occurring during the central hours of day. Although shade levels given were large enough to reduce the rate of CO_2 assimilation of both rubber and banana, reduced incidence of dynamic photoinhibition in both crops under shade would account, in part, for the improved growth of banana and rubber when intercropped.

Key words: Chlorophyll fluorescence, natural shade, photoinhibition, photosynthesis

Introduction

As natural forest species, rubber and banana would naturally regenerate under the shade of an overstorey canopy. However, with domestication as commercial crops, both crops have been cultivated under conditions rather different to that of their origin. Plants are usually established on land that has been cleared and so devoid of any overhead shade resulting in young plants being exposed to high radiation loads during establishment. There has been increasing evidence to suggest that

high incident radiation loads experienced under natural conditions can result in stress-induced depression of photosynthetic productivity of different crops (Powles, 1984; Baker *et al.*, 1994; Cornic, 1994).

In rubber/banana mixed cropping systems, banana overshadows rubber at early establishment phase and then both crops experience some level of mutual shading until rubber overshadows banana at *ca.* 4 years. Previous studies have shown that intercropping enhances the growth of

* Rubber Research Institute of Sri Lanka, Dartonfield, Agalawatta, Sri Lanka

** School of Agricultural and Forest Science, University of Wales, Bangor, UK

Photosynthesis of rubber and banana in shade

both rubber and banana (Rodrigo *et al.*, 1997; 2001) and it may be that plants benefit from the effects of shade in terms of reducing high temperature stress and/or light-induced damage to photosynthesis *i.e.* photoinhibition. Results from early studies (Rodrigo *et al.*, 1997; 2001) and discussions with rubber smallholders suggest that shade is an important factor for early growth of rubber and intercrops because of the effects of shade in reducing high radiation loads and improving soil moisture (Senevirathna, 2001). However, a severe reduction in incident radiation will reduce photosynthetic productivity of both rubber (Nugawela *et al.*, 1995) and banana (Israeli *et al.*, 1996; Eckstein *et al.*, 1997). High radiation induced photoinhibition indicated by the ratio of F_v/F_m of a vast range of tropical species has been recorded and shade has reduced the incidence of photoinhibition (Thiele *et al.*, 1998; Ishida *et al.*, 1999). Few, if any, studies on the high radiation-induced depression of photosynthesis of rubber and banana were recorded, except drought-induced photoinhibition of rubber was reported by Jacob *et al.* (1999). In the present research, shade imposed by natural vegetation, which provides sunfleck effect and reduced red/farred ratio (Chazdon and Fetcher, 1984; Percy, 1987) together with the reduced incident radiation, was used to determine the shade effects on photosynthetic performance of rubber and banana. It was hypothesised that the high radiation loads typically experienced in the tropics result in high light-induced photoinhibition and a

reduction in photosynthetic productivity of both rubber and banana.

Materials and methods

Details with respect to the establishment of the experiment were given in the part 1 of the paper (Senevirathna *et al.*, 2002).

Ambient temperature, rainfall, % relative humidity and total incident radiation of the experimental site (under open conditions) were monitored by an automatic weather station (Campbell Scientific Ltd., Leicestershire, UK.) from November 1999 to April 2001. Measurements were taken at every five minutes intervals and hourly means were recorded by a data logger (21X, Campbell Scientific Ltd., Leicestershire, UK).

The automatic weather station was only installed at the experimental site in May 2000 (*i.e.* six months after planting) because of malfunctioning of the data logger. Similarly, the temperature and humidity probe and rain gauge were out of range and malfunctioning for some time and so ambient temperature, relative humidity (%RH) and rainfall data were obtained from the Biometry Section of the Rubber Research Institute of Sri Lanka (RRISL) who has a weather station (Casella Co., UK.) situated within *ca.* 500 m of the experimental site. The %RH was measured using the 'wet' and 'dry' bulb technique.

Diurnal changes in leaf gas exchange

In order to observe the diurnal pattern of leaf gas exchange, measurements were taken at three

intervals in the day, *i.e.* morning (0900-1100 h), midday (1200-1400 h) and evening (1500-1700 h). Measurements were made opportunistically on bright sunny days (maximum photosynthetic photon flux density, PPFD of *ca.* 2100 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and on overcast days (maximum PPFD of *ca.* 1200 $\mu\text{mol m}^{-2}\text{s}^{-1}$) depending on weather conditions. Measurements were taken from two leaves of the uppermost fully developed, bright green whorl of rubber and from the mid portion of both sides of recently expanded third leaf of banana, using a LI-6200 portable photosynthesis system (Li-Cor, Inc., USA). Three replicate plants were randomly selected from each treatment and crop.

Diurnal changes in F_v/F_m

In order to determine the effects of shade and daily incident PPFD levels on photosynthetic efficiency of leaves, the ratio of variable to maximal fluorescence (F_v/F_m) was measured at two-hour intervals between 0700 and 1800 hours using a Plant Efficiency Analyser, PEA (Hansatech Instrument Ltd., UK). Prior to each set of F_v/F_m measurements, leaves from five replicate plants in each treatment were dark adapted for 25 minutes (Senevirathna, 2001) using leaf clips provided. The saturating light intensity of the PEA was adjusted to 70% and 50% for rubber and banana leaves, respectively (Senevirathna, 2001). Measurements were taken on clear days (maximum PPFD of *ca.* 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$).

Changes in F_v/F_m of artificially shaded and fully exposed leaves

Leaves in the unshaded control were artificially shaded in order to determine the extent to which high incident PPFD accounted for depressions in F_v/F_m in the unshaded leaves under field conditions. Five plants from each crop in the unshaded control were used. Two adjacent leaflets from the most recently expanded fully matured whorl of rubber and one side of the recently expanded third leaf of banana were selected in order to minimise any effects of leaf age and position on treatment response. One leaflet of rubber and a part of banana lamina were shaded artificially by placing a neutral white filter paper (80 gsm) at a distance of *ca.* 5 cm above the upper leaf surface. Prior to each set of F_v/F_m measurements, leaflets and lamina portions were dark adapted for a period of 25 minutes using leaf clips. F_v/F_m was measured every two hours from 0700 to 1800 hours together with measurements of incident PPFD and temperature of the same leaf using a Steady State Porometer, LI-1600 (Li-Cor Inc., USA.), in order to account the microclimatic changes as a result of artificial shading.

Time-course for recovery of F_v/F_m following exposure of leaves to high incident PPFD under field conditions

The rate of recovery of F_v/F_m following exposure of leaves to high incident PPFD, typical of those experienced under field conditions was studied using pot-grown plants of rubber and banana. Five potted rubber

Photosynthesis of rubber and banana in shade

plants that were six to seven months old, bearing two leaf whorls and potted new suckers of banana were placed at the site of the unshaded control treatment for *ca.* two months. Plants were fertilised as recommended (Samarappuli, 2001; Department of Agriculture, 1995). Watering was done every other day except in rainy seasons.

After two months, *i.e.* after full expansion of the third leaf whorl of rubber and at fifth leaf stage of banana, on a clear day when PPFD was *ca.* 1800-2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$ at midday, F_v/F_m of two leaves of the recently developed third whorl of each rubber plant and of fourth leaf of banana was measured after a period of 25 minutes dark adaptation using the PEA. Following the midday measurement, the plants were taken to the laboratory and recovery of F_v/F_m was monitored at 30 minutes intervals until a constant F_v/F_m (*i.e.* three consecutive measurements that were almost the same) was achieved, under controlled conditions of low PPFD of 162 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (± 2.7) and an air temperature of 27.0 °C (± 0.01).

Changes in F_v/F_m in relation to the laminar angle of banana

Diurnal changes in laminar angle (*i.e.* the angle between two halves to the midrib of the leaf from underside) of banana in each treatment were measured in the morning (0800-1000 h), midday (1200-1400 h) and evening (1600-1800 h) on a clear day together with the incident PPFD measurements. Five plants and second, third and fourth leaves, from each plant and treatment, were selected in order to represent the

top of the canopy, which is often exposed to direct sunlight. In order to test the extent to which the reduction in laminar angle of banana on clear days affect the degree of the depression in F_v/F_m , the laminar angle of plants in the unshaded treatment, which was expected to have a clear response, was kept at 180° and, F_v/F_m measurements were made diurnally. The most recently expanded third leaf, which was almost in the same position to the east-west direction, was selected from ten plants in the unshaded treatment. The mid portion of the laminar from five plants was kept at 180° and perpendicular to the midday solar radiation, with a light aluminium frame fitted to the abaxial surface of the leaf. The other five leaves were kept unaltered, and F_v/F_m measurements were taken in the morning (0800-1000 h), midday (1200-1400 h) and evening (1600-1800 h) from both altered and unaltered leaves. Prior to each set of measurements, leaves were dark adapted for 25 minutes with leaf clips provided.

Data analysis

Data analyses were performed using SAS statistical package and the Nested procedure (SAS Institute Inc., Cary, NC, USA). Diurnal changes of CO₂ assimilation, F_v/F_m and laminar angle of banana were analysed using analysis of variance (ANOVA). The mean separation of treatments was performed with Duncan's multiple range test (DMRT).

Results

Weather conditions of the

experimental site are summarised in Figure 1. Total rainfall was 5460 mm from 19th November 1999 (date of planting) until the end of April 2001 (Fig. 1a). The mean maximum and minimum air temperature for the experimental period was 31.9 (± 0.1) and 22.6 (± 0.1) °C, respectively, with an average temperature of 27.2 (± 0.1) °C (Fig. 1a). The mean relative humidity (%RH) was *ca.* 76.2% (± 0.5) during the period from November 1999 to November 2000 when monitoring was done using the wet and dry bulb technique. Continuous monitoring of %RH came into effect from November 2000 with the installation of the humidity probe (MP 100A, Campbell Scientific Ltd., UK); mean values resulted from the wet and dry bulb technique were *ca.* 10% less than that recorded with the humidity probe (Fig. 1b). Weekly mean incoming radiation during daylight hours ranged between 105 to 216 MJm⁻² with a mean of 172 (± 5) MJm⁻² for the experimental period (Fig. 1b).

The average CO₂ assimilation rates measured under sunny and overcast conditions showed that the rates were higher throughout day in unshaded plants of both rubber and banana compared to the shaded plants (Fig. 2; $p \leq 0.05$). The CO₂ assimilation rates were high in banana with a maximum of 20.9 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (± 1.0) compared to the maximum of 17.9 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (± 0.5) achieved in rubber (Fig. 2). The highest shaded rubber and banana showed the lowest rates of CO₂ assimilation throughout day ($p \leq 0.05$) whilst low and medium shade

treatments performed intermediate to the unshaded and high shade treatments (Fig. 2).

Figure 3 shows the diurnal changes in F_v/F_m of rubber and banana measured on bright sunny days together with incident PPFD and leaf temperature. Values of F_v/F_m showed a clear depression during the central hours of the day, followed by a trend of recovery towards evening in both rubber and banana. In general, diurnal values of F_v/F_m were always highest in the high shade treatment and lowest in the unshaded treatment (Fig. 3b,e; $p \leq 0.05$). F_v/F_m of unshaded leaves of rubber declined from 0.819 (± 0.004) in the early morning to 0.753 (± 0.008) at midday (Fig. 3b) whilst those values in banana were 0.818 (± 0.003) and 0.757 (± 0.006), respectively (Fig. 3e). In the high shade treatment, F_v/F_m ranged between 0.830 and 0.840 throughout the day in both rubber and banana (Fig. 3b,e). The corresponding leaf temperature of both crops was significantly higher in the unshaded treatment ($p \leq 0.05$) but there was no significant difference amongst three other shade treatments (Fig. 3c,f).

The midday decline in F_v/F_m of unshaded leaves of both rubber and banana on clear days was much less when leaves were subject to artificial shading (Fig. 4), with a rapid recovery in F_v/F_m to values similar to those observed early in the morning (Fig. 4b, e). Artificial shading reduced incoming radiation by 75-80% (Fig. 4a,d) and increased F_v/F_m maximally by 8% in rubber (Fig. 4b) and by 16% in banana (Fig. 4e) to the corresponding values in

Photosynthesis of rubber and banana in shade

unshaded leaves. Artificial shading also lowered the leaf temperature by a maximum of 2.4 °C in rubber and 2 °C

in banana compared with the unshaded leaves (Fig. 4c,f) as observed in the natural shade treatments (Fig 3c,f).

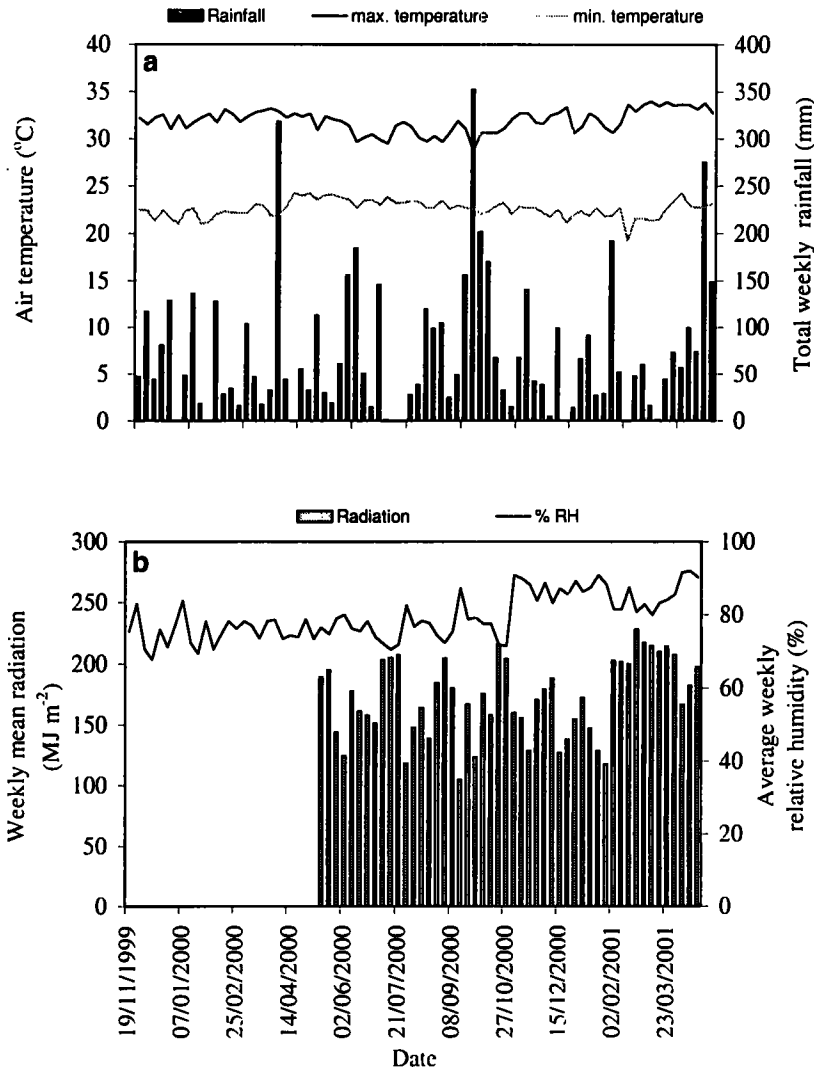


Fig. 1. Summary of weather conditions for (a) weekly rainfall, maximum and minimum air temperature, and (b) average weekly relative humidity (%RH) and mean radiation at the experimental site from 19th November 1999 (planting) to 30th April 2001 (end of measurements). Weekly mean radiation was calculated as the average of the total cumulative daily radiation for the photoperiod from 0800 to 1800 hours. Radiation data up to 16 May 2000 were not presented due to malfunctioning of the data logger.

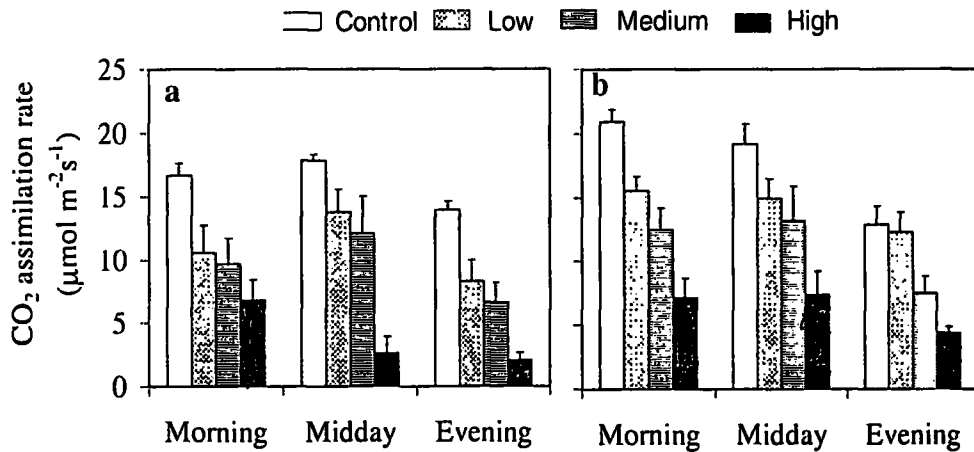


Fig. 2. Summary of the diurnal changes of CO₂ assimilation rates of (a) rubber and (b) banana in the unshaded control, low, medium and high shade treatments where the percentage reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Each value is the mean of 12 replicates \pm SE. measured on sunny (PPFD of ca. 2100 $\mu\text{mol m}^{-2}\text{s}^{-1}$) and overcast (PPFD of ca. 1200 $\mu\text{mol m}^{-2}\text{s}^{-1}$) conditions

Although there was a trend of recovery in F_v/F_m towards evening, the values observed in the evening have not been achieved to that of observed early in the morning, especially in rubber, except in the high shade treatment (Fig. 3b). Figure 5 summarises the analysis of the rate of recovery in F_v/F_m of sun-grown leaves of rubber and banana plants exposed to a high PPFD under field conditions (ca. 2000 $\mu\text{mol m}^{-2}\text{s}^{-1}$). At midday (HL), under field conditions, F_v/F_m ratio of rubber and banana leaves declined to 0.711 (± 0.016) and 0.746 (± 0.018), respectively, and was recovered to 0.808 (± 0.004) and 0.820 (± 0.003), respectively in rubber and banana within five to six hours of incubation under controlled PPFD ($162 \pm 2.7 \mu\text{mol m}^{-2}\text{s}^{-1}$) and temperature

(27 ± 0.01 °C) in the laboratory (Fig. 5).

The lamina angle of banana was significantly lower ($p \leq 0.01$) at midday than in the morning or evening, coinciding with incident PPFD (Fig. 6a, b). At midday, the lowest and highest values of lamina angle were observed in the unshaded and the highest shaded treatments, respectively (Fig. 6a, b). Towards evening, lamina angle increased and no significant treatment effect was observed ($p > 0.05$). Artificially holding lamina angle at 180° and perpendicular to the midday sun caused a small but not significant depression ($p > 0.05$) of F_v/F_m at midday, whilst towards the evening, F_v/F_m was recovered and the values were higher in the leaves that had natural altering of lamina angle ($p \leq 0.05$; Fig. 6c).

Photosynthesis of rubber and banana in shade

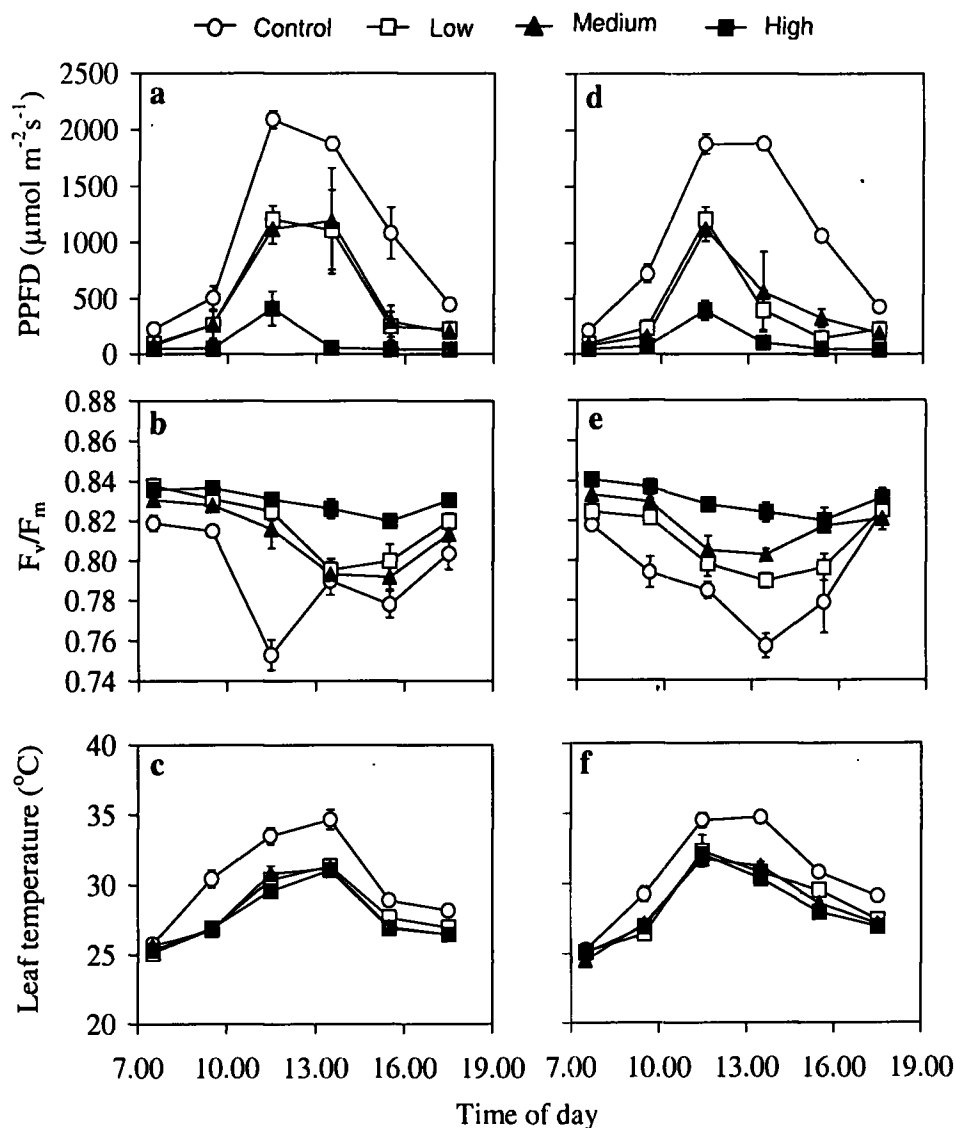


Fig. 3. Diurnal changes in photosynthetic photon flux density (PPFD) together with corresponding F_v/F_m and leaf temperature of rubber (a,b,c) and banana (d,e,f) in the unshaded control, low, medium and high shade treatments where the percentage reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Data represent the mean of five replicates \pm SE.

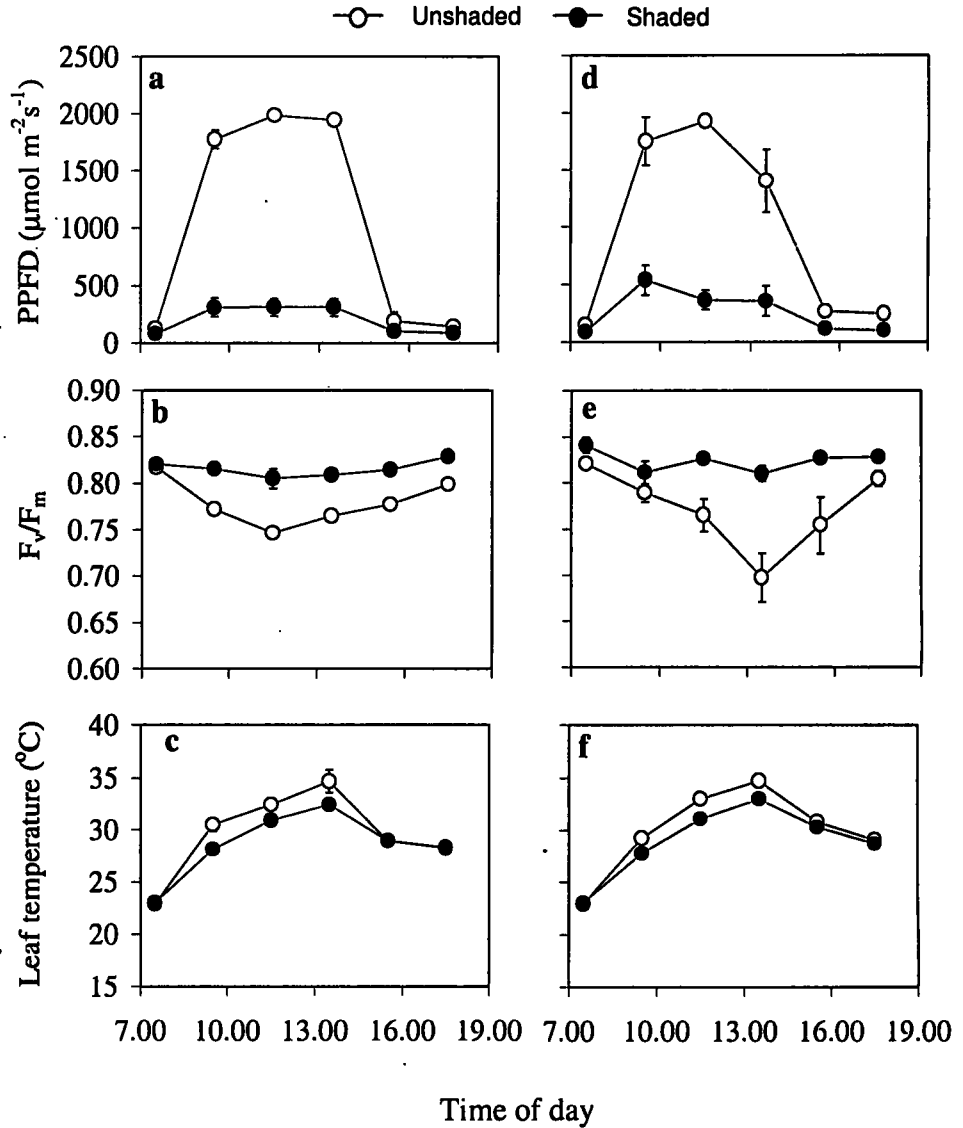


Fig. 4. Diurnal changes in photosynthetic photon flux density (PPFD) together with corresponding F_v/F_m and leaf temperature of unshaded and artificially shaded leaves of rubber (a,b,c) and banana (d,e,f) in the unshaded control treatment. Artificial shades using neutral white filters reduced incident radiation by 75-80%. Data represent the mean of five replicates \pm SE

Photosynthesis of rubber and banana in shade

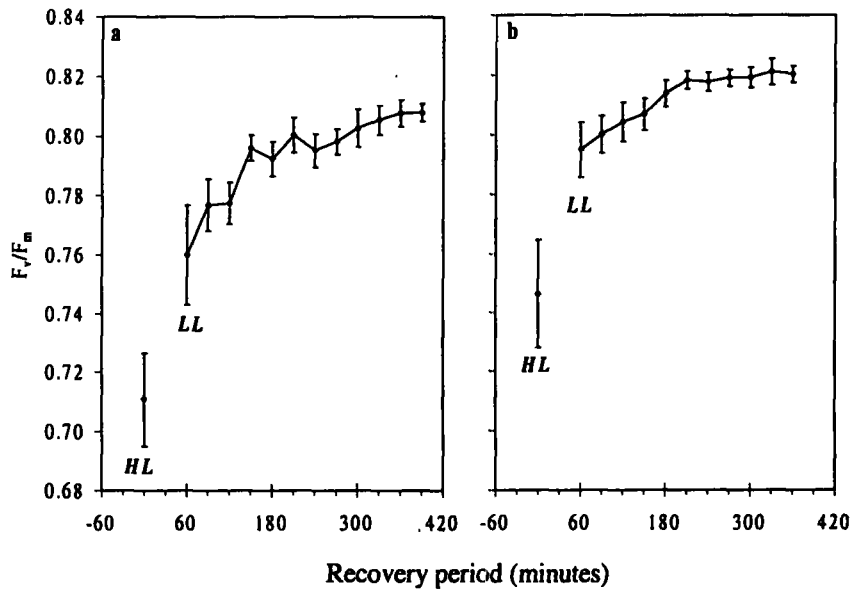


Fig. 5. Summary of the recovery in F_v/F_m of pot grown (a) rubber and (b) banana plants under full sunlight. Measurements at time=0 were taken at midday in the field (PPFD was ca. $1800-2000 \mu\text{mol m}^{-2}\text{s}^{-1}$) (HL) and then plants were transferred to the laboratory at time=60 mins. (LL). Conditions in the laboratory were: PPFD= $162 \mu\text{mol m}^{-2}\text{s}^{-1}$ (± 2.7) and air temperature= 27°C (± 0.01); light was provided by daylight quality fluorescent bulbs. Data represent the mean of 10 replicates \pm SE.

Discussion

The study has clearly shown that plants benefit from shades, particularly during the midday hours avoiding greater radiation loads. Photosynthetic efficiency of both rubber and banana crops, as indicated by F_v/F_m , was higher in shade than in unshaded plants throughout day with greatest difference during and/or after the midday hours (Fig. 3). Radiation loads received during study period (Fig. 1b) were typical to tropical field conditions and surely stressful to plants, and so the loss of potential photosynthetic productivity is high in plants grown

under full sunlight. In support of this, it has been observed that daily loss of carbon gain of sunlit leaves was higher than that of shade leaves of *Quercus coccifera* (Werner *et al.*, 2001). However, the shade levels given in the present study were over and above the requirements of plants with respect to alleviation of radiation stress, hence differences in chlorophyll fluorescence in sun lit and shaded plants were neither reflected by the rates of CO_2 assimilation (Fig. 2) nor the growth performance, (Senevirathna, 2001; Senevirathna *et al.*, 2002). Benefits of shade alleviated radiation stress have

been overridden by reduction in overall photosynthesis; therefore the ultimate dry matter production was poor in shaded plants.

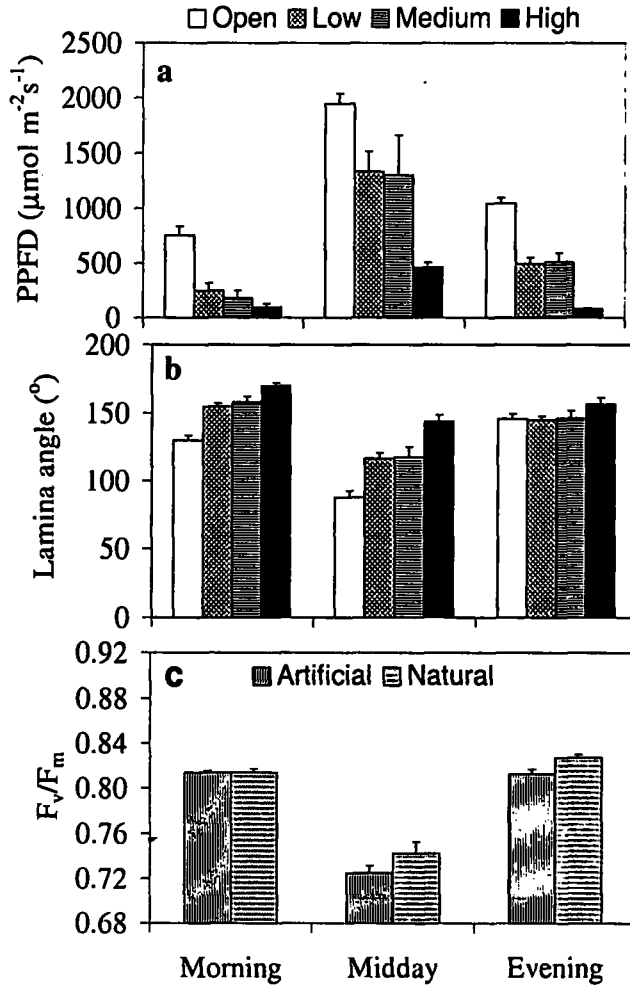


Fig. 6. Diurnal changes in (a) photosynthetic photon flux density (PPFD), (b) corresponding lamina angle of banana in the unshaded control, low, medium and high shade treatments where the % reduction in incoming radiation was 0, 33, 55 and 77%, respectively. (c) is the F_v/F_m of banana leaves in which the lamina angle was not manipulated (Natural) and was held at 180° (Artificial) with a support of a light wire frame in the unshaded control treatment. Data represent the mean of five replicates \pm SE.

Photosynthesis of rubber and banana in shade

Photoinhibition under stress conditions could be explained by down regulation of photosynthesis and/or damages at the photosystem, particularly PSII (Osmond, 1994). The effect of latter is quite permanent; hence generally show long-term effects resulting in clear depression in plant growth (*e.g.* Chilling induced photoinhibition – Baker *et al.*, 1994). Even if the unshaded plants were generally exposed to stressful solar radiation (Fig. 1b), no damage to the photosynthesis systems was observed as previously observed for many plants (Kitao *et al.*, 2000a). Therefore, the photoinhibition shown in the present study could be more attributed to the former type. Although there was a trend of recovery in F_v/F_m ratios of both rubber and banana towards the end of the day, complete recovery needs overnight incubation under natural field conditions on a clear day (Senevirathna, unpublished data). The recovery of midday depressed F_v/F_m of both crops achieved within five to six hours of incubation under controlled PPFD and temperature (Fig. 5), indicating that natural field conditions of tropics are too harsh to achieve a quick recovery.

The intensity of the incident PPFD and its effects on changes in crops' microclimate (*e.g.* leaf temperature) appeared to be responsible for the greater depression in F_v/F_m during the central hours of the day (Figs. 3 and 4). This was clearly shown by the increase in F_v/F_m in artificially shaded leaves in the plants grown under full sunlight corresponding with decline in incident PPFD and resulted leaf

temperature (Fig. 4). Similar to the observation made in the natural shade treatments (Fig. 3), the decline in leaf temperature by shading with white filters enabled to reduce the temperature stress on plants as observed by Kitao *et al.* (2000b) in some tropical species.

There is evidence that some plants alter the leaf angle to a position more or less parallel to the sun's rays in order to reduce incident radiation and hence absorption of excess PPFD (Bjorkman and Powles, 1981). Also, the decline in lamina angle of banana has been found to be correlated with the water status of leaves and may serve to prevent water loss through transpiration under high PPFD and high temperature conditions (Thomas and Turner, 1998). When lamina angle of banana was held at 180° and perpendicular to the midday solar rays, there was a trend of depression in F_v/F_m compared to that in the unaltered leaves (Fig. 6). Therefore, there is evidence that changes in lamina angle offer protection from dynamic photoinhibition of banana to a certain extent.

In conclusion, although improved growth of component crops in rubber/banana systems with high density planting of banana was observed possibly due to the reduced radiation stress created by mutual shading (Rodrigo *et al.*, 1997, 2001), in the present study even the lowest shade (33% reduction in incoming radiation) did not show a growth improvement over the unshaded plants (Senevirathna, 2001; Senevirathna, 2002). This is more likely due to the lower light levels experienced under shade treatments

throughout, compared with light levels of mutually shaded intercrop canopies. Nevertheless, both rubber and banana showed ability to reduce the degree of dynamic photoinhibition under shade conditions, which might, in part, contribute to an increase in carbon gain and hence productivity under mild shade conditions typical of that experienced in intercrops.

Acknowledgements

This publication is an output from a project of Plant Science Research Programme funded by the UK Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. Authors also wish to thank Mrs Wasana Wijesuriya, Biometrician of the Rubber Research Institute of Sri Lanka for her great assistance in analysing data and providing weather data.

References

- Baker, N R, Farage, P K, Stirling, C M and Long, S P (1994). Photoinhibition of crop photosynthesis in the field at low temperatures. In: *Photoinhibition of photosynthesis: from molecular mechanisms to the field*. pp. 349-363. (Eds. N R Baker and J R Bowyer), BIOS Scientific Publishers Ltd., UK.
- Bjorkman, O and Powles, S B (1981). Leaf movement in the shade species *Oxalis oregana*. I. Response to light level and light quality. *Carnegie Inst. Wash. Yearb.* **80**, 59-62.
- Chazdon, R L and Fetcher, N (1984). Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* **72**, 553-564.
- Cornic, G (1994). Drought stress and high light effects on leaf photosynthesis. In: *Photoinhibition of photosynthesis: from molecular mechanisms to the field*. pp. 297-313. (Eds. N R Baker and J R Bowyer), BIOS Scientific Publishers Ltd., UK.
- Department of Agriculture, Sri Lanka, (1995). *Planting Banana*. Department of Agriculture, Sri Lanka.
- Eckstein, K, Robinson, J C and Fraser, C (1997). Physiological responses of banana (*Musa* AAA; Cavendish subgroup) in the subtropics. VII. Effects of windbreak shading on phenology, physiology and yield. *Journal of Horticultural Science* **72**, 389-396.
- Ishida, A, Nakano, T, Matsumoto, Y, Sakoda, M and Ang, L H (1999). Diurnal changes in leaf gas exchange and chlorophyll fluorescence in tropical tree species with increasing light requirements. *Ecological Research* **14**, 77-88.
- Israeli, Y, Schwartz, A, Plaut, Z and Yakir, D (1996). Effects of light regime on $\delta^{13}\text{C}$, photosynthesis and yield of field grown banana (*Musa* sp.). *Plant, Cell and Environment* **19**, 225-230.
- Jacob, J, Annamalai, N K and Nataraja, K N (1999). Drought induced photo oxidative stress and inhibition in photosynthesis in *Hevea brasiliensis*. *Proceedings of the eleventh Kerala Science Congress*, February to March 1999, Kasaragod. pp. 445-448.
- Kitao, M, Lei, T T, Koike, T, Tobita, H and Maruyama, (2000a). Susceptibility to photoinhibition of three deciduous broadleaf tree species with different successional traits raised under various light regimes. *Plant, Cell Environ.* **23**, 81-89.
- Kitao, M, Lei, T T, Koike, T, Tobita, H, Maruyama, Y, Matsumoto, Y and Ang, L H (2000b). Temperature responses

Photosynthesis of rubber and banana in shade

- and photoinhibition investigated by chlorophyll fluorescence measurements for four distinct species of dipterocarp trees. *Physiologia Plantarum* **109**, 284-290.
- Nugawela, A, Ariyawansa, P and Samarasekara, R K (1995). Physiological yield determinants of sun and shade leaves of *Hevea brasiliensis*. *Journal of the Rubber Research Institute of Sri Lanka* **76**, 1-10.
- Osmond, C B (1994). What is photoinhibition? Some insights from comparisons of shade and sun plants. In: *Photoinhibition of photosynthesis: from molecular mechanisms to the field*. pp. 1-24. (Eds. N R Baker and J R Bowyer), BIOS Scientific Publishers Ltd., UK.
- Pearcy, R W (1987). Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understorey microenvironments. *Func. Ecol.* **1**, 169-178.
- Powles, S B (1984). Photoinhibition of photosynthesis induced by visible light. *Annual Review of Plant Physiology* **35**, 15-44.
- Rodrigo, V H L, Stirling, C M, Teklehaimanot, Z and Nugawela, A (1997). The effect of planting density on growth and development of component crops in rubber/banana intercropping systems. *Field Crops Research* **52**, 95-108.
- Rodrigo, V H L, Stirling, C M, Teklehaimanot, Z and Nugawela, A (2001). Intercropping with banana to improve fractional interception and radiation-use efficiency of immature rubber plantations. *Field Crops Research* **69**, 237-249.
- Samarappuli, L (2001). Nutrition. In: *Handbook of rubber Vol. 1: Agronomy*. pp. 156-175 (Eds. L M K Tillekeratne and A Nugawela), Rubber Research Institute of Sri Lanka, Agalawatta, Sri Lanka.
- Senevirathna A M W K (2001). The influence of farmer knowledge, shade and planting density on smallholder rubber/banana intercropping in Sri Lanka. *PhD thesis*. School of Agricultural and Forest sciences, University of Wales, Bangor, UK.
- Senevirathna, A M W K, Stirling, C M, Rodrigo, V H L, Karunathilake, P K W and Pathirana, P D (2002). Is shade important in rubber based cropping systems? Part 1. Effect of shade on growth, dry matter partitioning and adaptation of rubber and banana. *Journal of the Rubber Research Institute of Sri Lanka* **85**, 27-38.
- Thiele, A, Krause, G H and Winter, K (1998). *In situ* study of photoinhibition of photosynthesis and Xanthophyll cycle activity in plants growing in natural gaps of the tropical forests. *Australian Journal of Plant Physiology*. **25**, 189-195.
- Thomas, D S and Turner, D W (1998). Leaf gas exchange of droughted and irrigated banana *cv.* Williams (*Musa sp.*) growing in hot, arid conditions. *Journal of Horticultural Science and Biotechnology* **73**, 419-429.
- Werner, C Ryel, R J, Correia, O and Beyschlag, W (2001). Effects of photoinhibition on whole plant carbon gain assessed with a photosynthesis model. *Plant and Cell Environment* **24**, 27-40.
- Address for correspondence:* Dr A.M.W.K. Senevirathna, Botanist, Rubber Research Institute of Sri Lanka, Dartonfield, Agalawatta, Sri Lanka.
E-mail: wasan@sltnet.lk