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ACCLIMATION OF PHOTOSYNTHESIS AND GROWTH OF BANANA (*MUSA* SP.) TO NATURAL SHADE IN THE HUMID TROPICS

By A. M. W. K. SENEVIRATHNA†, C. M. STIRLING‡ *and* V. H. L. RODRIGO

Rubber Research Institute of Sri Lanka, Dartonfield, Agalawatta 12200, Sri Lanka and ‡School of Agricultural and Forest Sciences, University of Wales, Bangor, LL57 2UW, United Kingdom

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SUMMARY

Growth and photosynthetic performance of banana (*Musa* sp.) grown in three levels of natural shade (33, 55 and 77% reduction in incoming radiation) were compared to an unshaded control treatment. Net CO_2 assimilation rates generally decreased with increasing shade. Chlorophyll fluorescence revealed short-term dynamic photoinhibition under high light conditions but no evidence of sustained photoinhibitory damage to photosystem II. Dynamic photoinhibition decreased with increasing shade, with the greatest depression in the variable to maximal fluorescence ratio (F_v/F_m) occurring in unshaded plants during the middle of the day. Specific leaf area and leaf area ratio increased proportionately with increasing shade, whilst the chlorophyll a/b ratio decreased, reflecting a greater efficiency of light utilization under shady conditions. The optimum shade level for photosynthetic productivity would be one at which the level of photosynthetic photon flux density (PPFD) is high enough to saturate CO_2 assimilation but low enough to induce shade acclimation and to reduce photoinhibition. Under the conditions studied here, the saturation level of PPFD was around 1000 μmol m^{-2} s^{-1}, a light level typical of the tree-based intercropping systems in which banana is commonly grown in the tropics.

INTRODUCTION

Banana is commonly grown in plantations as a monocrop, or in mixed cropping systems, under tropical and subtropical conditions. In mixed and high density cropping systems (Robinson and Nel, 1988; Rodrigo *et al.*, 1997; 2001), banana may experience mutual shading, and so benefit from changes in microclimate such as small reductions in photosynthetic photon flux density (PPFD), air temperature, turbulence and evaporative demand (Barradas and Fanjul, 1986). One of the most common companion crops grown with rubber in Sri Lanka is banana. Previous studies showed that banana growth improved when intercropped at high densities with rubber, with an increase in light interception and radiation use efficiency, possibly due to the benefits conferred by greater mutual shading in dense canopies (Rodrigo *et al.*, 1997; 2001). Other studies have reported negative impacts of shade on growth and photosynthetic productivity of banana (Israeli *et al.*, 1996; Robinson and Nel, 1988).

There is some evidence of acclimation of banana to maximize light capture under low light conditions; for example, banana grown in shade has thinner leaves and

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†Corresponding author: wasan@sltnet.lk, dirrri@sltnet.lk

increased chlorophyll content (Israeli *et al.*, 1996). Such acclimation improves the efficiency of light absorption and utilization by leaves (Anderson and Osmond, 1987). However, there are no reports of shade acclimation in terms of dry matter partitioning of banana.

Although numerous studies exist dealing with high temperature effects on banana, little is known of photoinhibition response to high radiation. Plants grown under drought conditions showed a decline in net photosynthesis and F_v/F_m compared to irrigated plants, indicating a drought-driven photoinhibition in banana leaves (Thomas and Turner, 1998; 2001). Since high PPFD has been shown to cause photoinhibition in a range of tropical species (Senevirathna *et al.*, 2003; Valladares and Pearcy, 1997), similar effects may be expected for banana, given the potentially high light environments in which it is grown. In such environments, the strong radiation-induced depression of photosynthesis may serve as a protective mechanism to avoid photoinhibitory damage.

All the shade experiments on banana so far reported have involved the use of artificial shades (e.g. Israeli *et al.*, 1996). Artificially manipulated shade reduces the incident PPFD but has little effect on spectral quality with no changes in the red to far-red ratio, unlike that observed in the understorey of natural vegetation where sunflecks contribute significantly to daily CO_2 assimilation (Valladares and Pearcy, 1997). In order to address the limitations of earlier shade studies, we assessed the effects of different shade levels on photosynthetic performance and shade acclimation of banana using natural shade provided by the canopies of rubber plantations.

MATERIALS AND METHODS

Experimental site

The experiment was conducted on the Dartonfield estate of the Rubber Research Institute of Sri Lanka (RRISL), at Agalawatta (6°32′N, 80°09′E, alt. 12 m asl), in the district of Kalutara of the low country wet zone of Sri Lanka. The soil is an Ultisol, with a silty-clay-loam texture and strong brown to yellowish-red in colour (Senevirathna *et al.*, 2003; Yogaratnam, 1983).

Experimental design

The experiment comprised four shade treatments, i.e. 0, 33 ± 1.0, 55 ± 0.5 and $77 \pm 0.7\%$ reduction in full sunlight and hereinafter referred to as unshaded control, low, medium and high shade treatments, respectively. Natural shade was imposed by selecting existing mature rubber plantations, and the different shade levels were achieved as a result of the age and inter-row spacing of rubber, and by selective pruning of branches of the mature rubber trees (Senevirathna, 2001). An open area close to the shaded sites was selected for the unshaded control treatment. Shade levels were monitored by a ceptometer (Delta-T Devices Ltd, Cambridge, UK) and by installing two solarimeters per treatment plot fixed above the canopies of banana plants and connected to the data logger (21 X, Campbell Scientific Ltd, Loughborough, UK) of the weather station (Campbell Scientific Ltd). A nested model was used as the experimental design, and each plant was considered as a single tree plot.

Field establishment and crop husbandry

The most common variety of banana in the wet zone of Sri Lanka, Embul, which belongs to the triploid genome group AAB, was selected for the study. Pre-treated rhizomes with ca. 0.3 m long pseudostems (25 per treatment) were planted in single rows between the rows of mature rubber, keeping an intra-row spacing of 3.0 m. In the unshaded control treatment, banana was planted at an intra- and inter-row spacing of 3.0 m and 4.0 m, respectively. To avoid competition with the roots of the mature rubber trees used to provide natural shade and to minimize variability in rooting conditions, all experimental plants were planted in soil-filled pits lined with a double layer of polythene film of gauge 500 (Musajee Pvt. Ltd., Colombo, Sri Lanka). Soil pits were excavated to a depth of 1 m and to a diameter of 1.8 m. All particles greater than 15 cm^3 were removed from the excavated soil, and the pits were refilled according to the original soil profile. Fertilizer was applied according to recommendations, and manual weeding was undertaken when required (Senevirathna, 2001).

Leaf gas exchange

Carbon dioxide assimilation rates were measured for a healthy, green, recently expanded third leaf in the canopy in each treatment at about 6 months after planting (MAP) together with the PPFD incident on leaves, using a LI-6200 photosynthesis system (Li-Cor Inc., Lincoln, NE, USA). Three replicate plants were selected from each treatment and gas exchange was measured at three intervals in the day, i.e. morning (08:30–10:30 hours), midday (11:00–13:00 hours) and evening (15:00–17:00 hours). Instantaneous measurements of leaf gas exchange were made on bright sunny days (maximum PPFD ca. 2100 μmol m^{-2} s^{-1}) and on overcast days (maximum PPFD ca. 1200 μmol m^{-2} s^{-1}) depending on the weather conditions of the experimental site.

Chlorophyll fluorescence

In order to determine the effects of daily incident PPFD levels on photosynthetic capacity of leaves under different light levels, the ratio of variable fluorescence (F_v), i.e. the difference between the maximal (F_m) and initial (F_o) fluorescence ($F_m - F_o$), to maximal (F_m) fluorescence, F_v/F_m, was measured at two-hour intervals between 07:00 and 18:00 hours using a Plant Efficiency Analyser (PEA) (Hansatech Instruments Ltd., Kings Lynn, UK). Prior to each set of F_v/F_m measurements, leaves from five replicate plants in each treatment were dark adapted for 25 min using the leaf clips provided. The saturating light intensity of the PEA (flash used to reduce fully the primary electron acceptor) was adjusted to 50%, as determined for banana leaves during preliminary experiments (Senevirathna, 2001). Measurements were taken on clear days (maximum PPFD of ca. 2100 μmol m^{-2} s^{-1}) and overcast days (maximum PPFD of ca. 1200 μmol m^{-2} 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 short-term shading accounted for alleviation of photoinhibition in the unshaded leaves under field conditions. The most recently expanded third leaf from five plants with leaves in the same plane of projection was selected in order to minimize any effects of leaf age and position on treatment response. One part of the middle of the lamina was shaded artificially by placing a neutral white filter paper at a distance of ca. 5 cm above the upper leaf surface throughout the day. Measurements of F_v/F_m were made from the shaded portion and an adjacent portion of the same half of the lamina, which was exposed to direct insolation. Prior to each set of F_v/F_m measurements, leaves were dark adapted for a period of 25 min using leaf clips. F_v/F_m was measured every two hours from 07:00 to 18:00 hours together with measurements of incident PPFD.

Analysis of leaf chlorophyll

Chlorophyll *a*/*b* ratio and total chlorophyll analyses were carried out for plants grown in the four shade treatments in order to determine the effect of shade on leaf chlorophyll. Lamina pieces of the most recently expanded third leaf from five plants in each treatment were harvested early in the morning at ca. 12 MAP. In the laboratory, 5 g of fresh leaf tissue was taken and cut into small pieces, ground with 80% aqueous acetone and the pigments were extracted at room temperature (27 °C) for about two hours. The extracts were then centrifuged at 500 *g* for five min, and the resultant supernatant separated from the precipitate by filtering through a Whatman No. 1 filter paper. The absorbance of the supernatant was measured using a spectrophotometer (M 330, Camspec, Cambridge, UK) at wavelengths 645 and 663 nm, using 80% acetone as the blank, and total chlorophyll and chlorophyll *a*/*b* were calculated (Hipkins and Baker, 1986).

Growth analysis

Using destructive sampling, both above- and below-ground dry matter was measured at seven MAP using mother plants and again at 17 MAP using the first ratoon crop, which is produced by the rhizome of mother plants. Five plants were randomly selected from each treatment for the growth analysis. Selected plants were completely uprooted and the total fresh weights of the components (leaves, pseudostem, rhizome and roots) were measured separately immediately after harvest. A sub-sample of 40% of the total fresh weight from each component was used for the dry matter determination (Rodrigo *et al.*, 1997). Samples were dried at 80 °C to a constant weight and total dry weights recorded. The area of each leaf was estimated according to the equation, leaf area = maximum length × maximum width × 0.755, after Rodrigo *et al.* (1997). Leaf area ratio (LAR, $m^2\ kg^{-1}$), specific leaf area (SLA, $m^2\ kg^{-1}$) and leaf weight ratio (LWR, $kg\ kg^{-1}$) were calculated as described by Hunt (1978).

Data analysis

Plant dry weights, LAR, SLA, LWR, diurnal changes in CO_2 assimilation and F_v/F_m were analysed with the nested procedure of SAS software (SAS Institute Inc., Cary, NC, USA). The procedure analysis of variance (ANOVA) was used for data analysis. The mean separation of treatments was performed with Duncan's multiple range test for the comparison of treatment effects.

RESULTS

CO_2 assimilation

PPFD incident on shaded plants was low throughout the day compared to the unshaded control, both on sunny and overcast days (Figure 1a,b). PPFD reached a mean maximum of 1801 (± 171) and 810 (± 252) μmol m^{-2} s^{-1} under clear sky and overcast conditions, respectively. Corresponding with the diurnal variation in PPFD, CO_2 assimilation rates were generally lower in the shade treatments than in the control (Figure 1c,d).

The highest CO_2 assimilation rate (21.5 μmol m^{-2} s^{-1}) under clear sky conditions was recorded in the unshaded control in the morning with assimilation rates significantly higher ($p < 0.001$) than in shade treatments. A similar pattern of CO_2 assimilation was observed in all the shade treatments, even under overcast conditions (Figure 1d). Furthermore, the highest shade treatment showed the lowest CO_2 assimilation rates throughout the day, both under sunny and overcast conditions (Figure 1c,d).

Chlorophyll fluorescence

The ratio of F_v/F_m showed a clear midday depression and recovery towards evening on both sunny and overcast days, with the midday depression greatest under clear sky conditions coinciding with the diurnal peak in PPFD (Figure 2). The highest and lowest values of F_v/F_m were recorded in the high shade and unshaded control, respectively, throughout the day and under both sunny and overcast conditions ($p < 0.001$). Under sunny conditions, F_v/F_m of the control declined from 0.818 (± 0.003) in the early morning to 0.757 (± 0.006) in the afternoon (13:00–14:00 hours). Values of F_v/F_m varied little during the day in the highest shade treatment with a range of between 0.84 and 0.82 both under clear sky and overcast conditions (Figure 2c,d). Low and medium shade produced more or less similar results, under both sunny and overcast conditions, except between 13:00 and 16:00 hours on the sunny day when the low shade treatment showed a greater depression in F_v/F_m ($p < 0.01$) than the medium shade plants (Figure 2c,d).

The midday decline in F_v/F_m was significantly less ($p < 0.001$) when leaves in the control were artificially shaded and F_v/F_m recovered rapidly in these leaves at the end of the day. Artificial shading reduced incoming radiation by 75–80% and increased F_v/F_m maximally by 16% at 13:00–14:00 hours (Figure 3a,b). Artificial shading lowered leaf temperature too, by a maximum of 2 °C (Figure 3c).

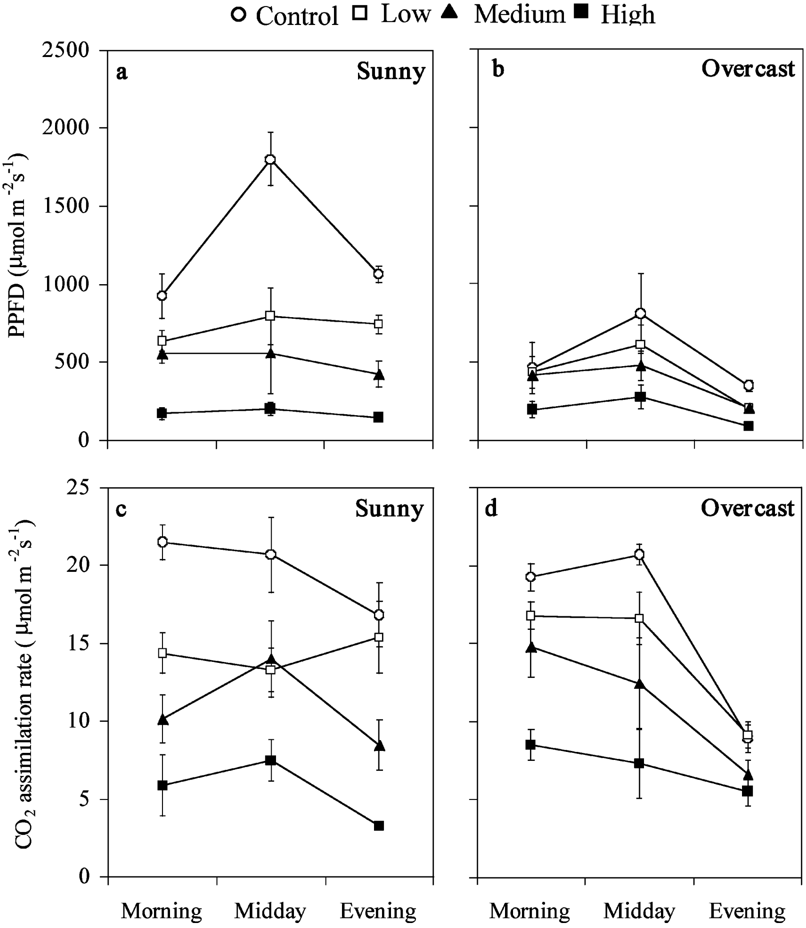

Figure 1. Diurnal changes in photosynthetic photon flux density (PPFD) on (a) sunny and (b) overcast days, and corresponding CO_2 assimilation rates on the same (c) sunny and (d) overcast days for banana in the unshaded control, low medium and high shade treatments where the reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Each value is the mean of six measurements ± *s.e.* Morning, midday and evening measurements were taken between 08:30 and 10:30 hours, 11:00 and 13:00 hours, and 15:00 and 17:00 hours, respectively.

Partitioning of dry matter

Total dry matter (TDM) production at seven MAP decreased with increasing shade (Figure 4a). However the first ratoon crop (17 MAP) showed a similar TDM production in the control and medium shade treatments, which were both significantly higher ($p < 0.01$) than the TDM of the low and high shades (Figure 4a). At seven MAP, the unshaded control produced 3.58 (± 0.72) kg dry matter, which was on average three-times greater than in shade treatments (Figure 4a). Furthermore, a linear relationship between cumulative incident radiation and cumulative dry matter production was observed for the 17-month period (Figure 4b, $r^2 = 0.848$). SLA increased ($p < 0.01$) with increasing shade at seven MAP; at 17 MAP, the high shade treatment showed apparently a higher ($p < 0.01$) SLA over the other shade treatments (Table 1). Similar

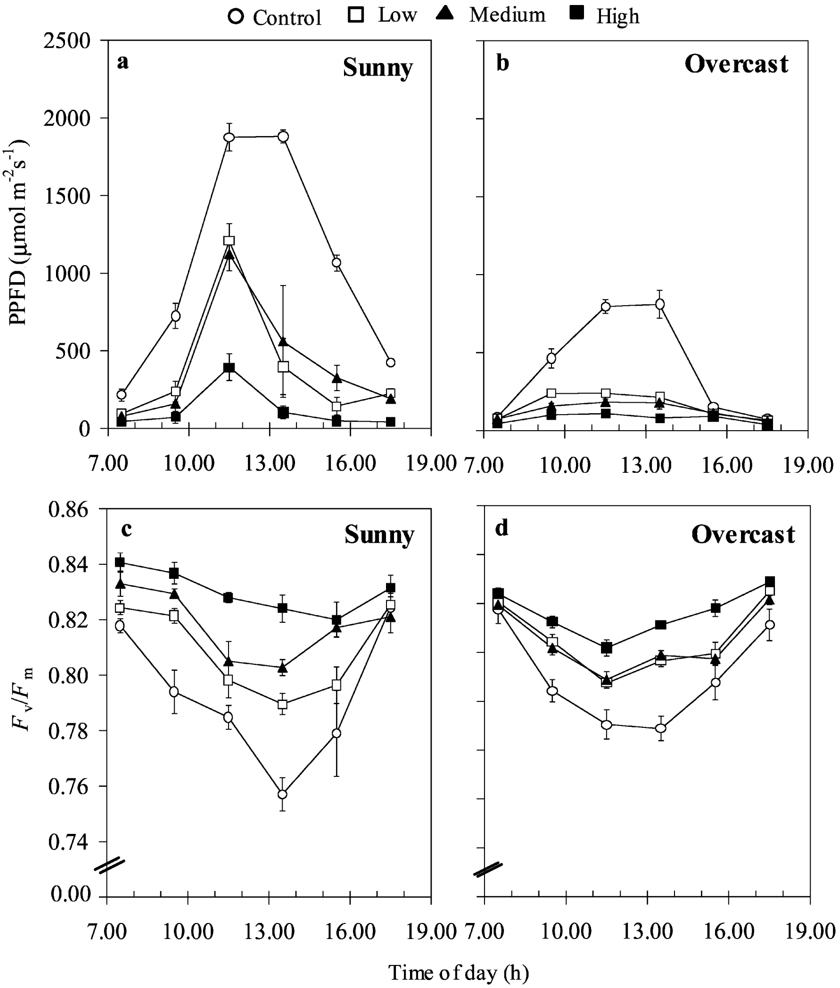

Figure 2. Diurnal changes in photosynthetic photon flux density (PPFD) on (a) sunny and (b) overcast days, and corresponding F_v/F_m ratios on the same (c) sunny and (d) overcast days for banana in the unshaded control, low medium and high shade treatments where the % reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Each value is the mean of five measurements ± *s.e.*

to SLA, treatments effects on LAR were most prominent at seven MAP when LAR increased significantly with shade ($p < 0.001$). In the ratoon crop, no consistent difference between treatments was observed with the exception of the high shade treatment where LAR was always greater ($p < 0.01$). LWR of banana decreased from seven to 17 MAP, but no significant treatment effect was observed (Table 1).

Chlorophyll content

Total chlorophyll concentrations tended to be higher in the shaded treatments than in the unshaded control but, unexpectedly, chlorophyll concentration was low in the highest shade treatment compared to the low and medium shade treatments

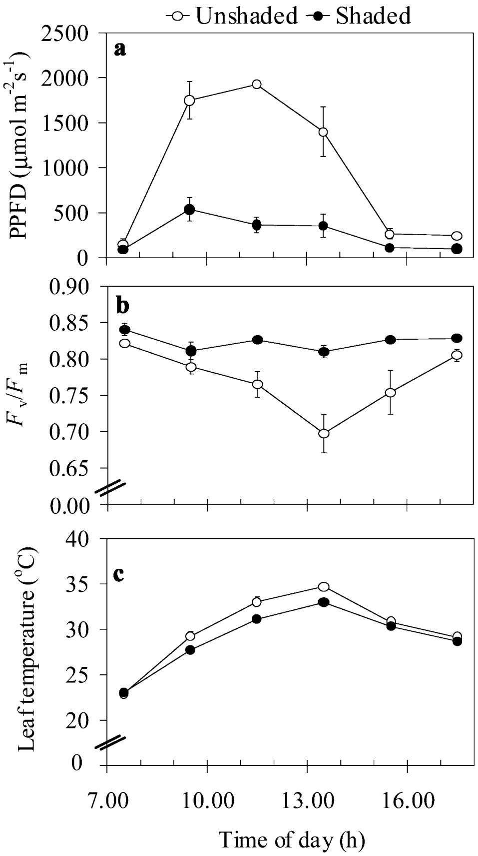

Figure 3. Diurnal changes in (a) photosynthetic photon flux density (PPFD), and corresponding (b) F_v/F_m ratios and (c) leaf temperature of banana leaves of unshaded and artificially shaded parts of leaves in the unshaded control treatment. Each value is the mean of five measurements ± *s.e.* Shades were provided by filter paper positioned 5 cm above the upper surface of leaves.

Table 1. Summary of specific leaf area (SLA), leaf area ratio (LAR) and leaf weight ratio (LWR) of banana at seven (mother crop) and 17 (first ratoon crop) months after planting (MAP) in the unshaded control, low medium and high shade treatments where the % reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Data represent the means of five replicate plants ± *s.e.*

	Shade treatment	SLA	LAR	LWR
7 MAP (Mother crop)	Control	10.9 ± 1.3	3.1 ± 0.3	0.29 ± 0.02
	Low	12.4 ± 0.8	4.3 ± 0.2	0.35 ± 0.02
	Medium	16.2 ± 1.3	5.8 ± 0.6	0.35 ± 0.01
	High	17.3 ± 1.5	6.5 ± 0.4	0.38 ± 0.03
17 MAP (First ratoon crop)	Control	10.2 ± 1.1	2.5 ± 0.3	0.26 ± 0.04
	Low	10.0 ± 0.3	1.7 ± 0.1	0.17 ± 0.01
	Medium	11.3 ± 0.6	3.0 ± 0.3	0.26 ± 0.02
	High	14.9 ± 1.6	3.8 ± 0.4	0.26 ± 0.01

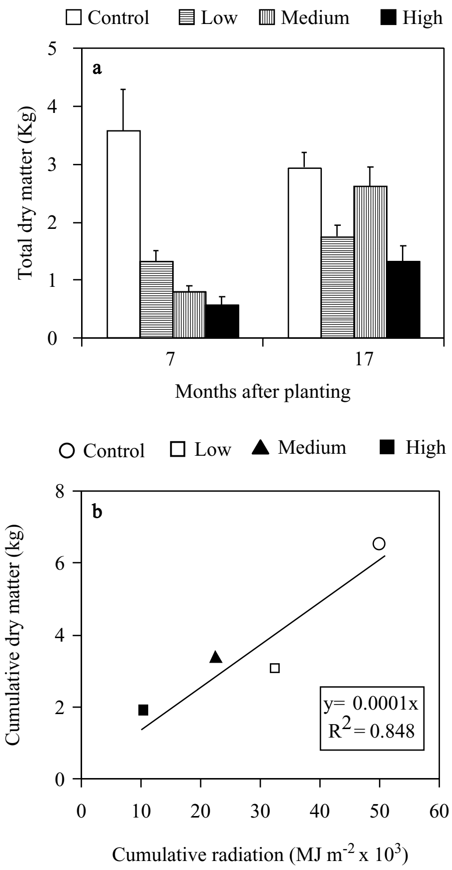

Figure 4. Summary of the dry matter production of banana where (a) is the total dry matter per plant at 7 (mother crop) and 17 (first ratoon crop) months after planting and (b) is the relationship between cumulative dry matter production and cumulative incident radiation for the period in the unshaded control, low medium and high shade treatments where the % reduction in incoming radiation was 0, 33, 55 and 77% respectively. Data represent the mean of five replicate plants ± *s.e.*

(Figure 5a). However, the chlorophyll *a*/*b* ratio declined with increasing shade from a maximum of 2.30 (± 0.19) in the control to 1.94 (± 0.02) in the high shade treatment (Figure 5b).

DISCUSSION

Growth and physiological performance of banana grown under shade differed from that of plants grown under full sunlight. Rates of photosynthesis revealed that unshaded plants had the highest assimilation capacity of all groups of plants. Assimilation of CO_2 measured under sunny and overcast conditions (Figure 1) indicated that PPFD incident on control plants on bright sunny days was far above the saturation levels; hence, there was little variation in CO_2 assimilation between sunny and overcast conditions. Photosynthetic light saturation of banana grown under full sunlight in this research was

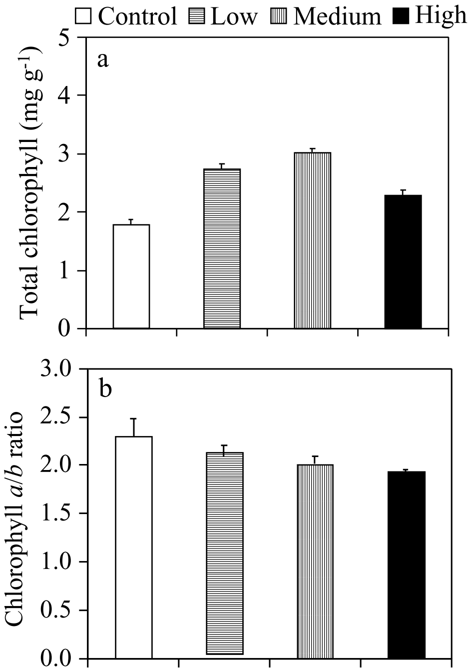

Figure 5. Summary of the chlorophyll analysis of banana leaves at 12 months after planting where (a) is the total and (b) is the *a*/*b* ratio of chlorophyll in the unshaded control, low medium and high shade treatments where the % reduction in incoming radiation was 0, 33, 55 and 77%, respectively. Data represent the mean of five replicates ± *s.e.*

ca. 1000 μmol m^{-2} s^{-1}, similar to that observed by Rodrigo *et al.* (2001) under similar tropical conditions. As indicated by the lower F_v/F_m ratios, excessive PPFD incident on banana leaves, especially during the central hours of the day, resulted in greater dynamic photoinhibition in unshaded plants (Figure 2). Moreover, artificial shading of leaves in the unshaded control treatment showed that even short-term shading helps to alleviate high radiation stress in banana (Figure 3). The rapid recovery in F_v/F_m towards the end of the day in the unshaded control (Figure 2, 3), suggested that the midday depression in F_v/F_m was most likely due to dynamic photoinhibition rather than photoinhibitory damage to photosystem II, as observed for other tropical crops (Senevirathna *et al.*, 2003). This phenomenon is a photoprotective mechanism rather than photodamage to the photosystem.

Although depression in F_v/F_m has been recorded in relation to low temperature (Damasco *et al.* 1997), reports on high-light-induced photoinhibition of banana are limited compared to other tropical plants (e.g. Ishida *et al.*, 1999; Senevirathna *et al.*, 2003). It was clear that the extent of high-light-induced photoinhibition was limited in plants grown under heavy shade. The reduction in incident PPFD in shaded treatments resulted in a corresponding reduction in TDM (Figure 4a), and this was supported by the linear correlation between cumulative incident radiation and cumulative dry matter production (Figure 4b). The apparent anomaly in TDM of shaded treatments where values were higher in the medium than the low and high shade treatments during the ratoon crop period, i.e. at 17 MAP (Figure 4a) may have been due to the differences in times of initiation of the first ratoon crop under different shade levels. However, cumulative dry matter production at seven and 17 MAP showed similar values in low and medium shade treatments.

Although TDM was reduced under shade conditions, banana showed an ability to acclimate to shade with an increase in SLA with increasing shade (Table 1). The production of thinner leaves under shade is an acclimation to enhance the efficiency of light utilization in shaded environments (Evans and Poorter, 2001). Increased LAR with increasing shade resulted from an increased ratio of dry matter partitioned to leaves under shade. LWR did not vary much across shade treatments, as both SLA and LAR changed in direct proportion to the density of shade. In addition to the shade acclimations in terms of increased SLA and LAR, the chlorophyll *a/b* ratio of leaves decreased under shade (Figure 5). This reflected the increased association of chlorophyll with the light harvesting complexes, which are rich in chlorophyll *b* (Evans and Poorter, 2001), in order to increase the efficiency of light harvesting in shade environments.

Since incident PPFD on unshaded plants was far above the saturation levels for photosynthesis, dynamic photoinhibition was greatest in plants that received full sunlight on bright sunny days revealing that photoprotection occurs in banana without damage to the photosystems. Although this study demonstrated that banana has the ability to acclimate to shade and to reduce dynamic photoinhibition under shade, the PPFD incident on the plants even in the lowest shade was not high enough to reflect such benefits in terms of dry matter accumulation. Therefore, mild shade in which the level of PPFD is high enough to saturate CO_2 assimilation and low enough to induce shade acclimation will help to optimize the photosynthetic productivity of banana.

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