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Effect of radiation quality on growth and photosynthesis of *Acacia mangium* seedlings

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Abstract

Radiation quality was an important environmental cue to stimulate seed germination in *Acacia mangium*. The photosynthetic CO_2 assimilation rate, dark respiration rate, total biomass, and relative growth rate of seedlings grown under monochromatic radiation were significantly lower than those of seedlings grown under full spectrum radiation. Blue and red radiation induced shade-avoidance and shade-tolerant responses of *A. mangium* seedlings, respectively.

Additional key words: biomass; blue and red radiation; dark respiration; germination; relative growth rate; shade avoidance and tolerance; stomatal conductance; true leaf.

Introduction

The irradiation in nature is very complex; the spectral quality (relative photon distribution at different wavelengths) of natural sunlight varies greatly with different locations on earth and the time of day (McNellis and Deng 1995). Plants perceive different radiation quality *via* different photoreceptors. These photoreceptors play important roles in germination, seedling establishment, and shade avoidance (Kendrick and Kronenberg 1994, Smith 1995), for instance. There are three main photoreceptors in higher plants: phytochromes, which absorb photons principally in the 600–800 nm region (Quail 1994), the blue radiation (BR) photoreceptors, which absorb radiation in the 300–500 nm region (Kaufman 1993), and the UV radiation photoreceptors, which absorb light between 290–300 nm (Kendrick and Kronenberg 1994).

Changes in radiation quality, in terms of the ratio of red radiation (RR) to far red radiation (FR), occur naturally within the forest canopy, as the transmitted radiation and reflected radiation on a forest floor have lower ratios of red to far-red photons than does incident radiation on the forest canopy (Kozlowski *et al.* 1991, Chazdon *et al.* 1996). The influence of RR:FR ratio on the photosynthetic characteristics of plants is relatively small, compared with that of radiation quantity (Schmitt and Wulff 1993, Hinsberg and Tienderen 1997, Lee *et al.* 1997). The perception of radiation quality, in terms of RR:FR, by phytochromes provides plants with a sensitive mean of detecting and responding to vegetation shade, and allows them to sense future competition, thus triggering morphological and physiological responses to avoid shading (Ballaré *et al.* 1987, 1990, Kendrick and Kronenberg 1994, Smith and Whitelam 1997).

There are differences in the wavelength composition between the radiation in open habitats and shaded environments. When radiation passes through a forest canopy, green and far-red wavelengths are preferentially transmitted or reflected, while red and blue wavelengths are preferentially absorbed (Bukhov *et al.* 1995, Tinoco-Ojanguren and Pearcy 1995). Thus, some studies investigated the effects of different wavelengths on plant growth and development (*e.g.* Eskins 1992, Milivojević and

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Abbreviations: BR – blue radiation; Chl – chlorophyll; CI – compensation irradiance; CMR – cotyledon mass ratio; F_v/F_m – potential photochemical efficiency of photosystem 2 under dark-adapted conditions; $\Delta F/F'_m$ – effective PS2 efficiency under light-adapted conditions; g_s – stomatal conductance; LAR – leaf area ratio; LMR – leaf mass ratio; NPQ – non-photochemical quenching *via* xanthophyll cycle; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; q_N – non-photochemical quenching; q_P – photochemical quenching; R_D – dark respiration rate; RGR – relative growth rate; RMR – root mass ratio; RR – red radiation; R/S – root to shoot ratio; SI – saturation irradiance; SLA – specific leaf area; SMR – stem mass ratio; WL – "white light"; WUE – water use efficiency; YR – yellow radiation.

Tyszkiewicz 1992, Brown *et al.* 1995, Maas *et al.* 1995). For example, Eskins (1992) reported that *Arabidopsis thaliana* plants grown under BR flowered earlier than those grown in RR; moreover, BR played an important role in the regulation of floral initiation and morphology of these plants. Brown *et al.* (1995) showed that *Capsicum annuum* plants, grown under RR-emitting diodes, exhibited lower irradiance-saturated rates of photosynthetic CO_2 fixation and total plant biomass than plants grown under a full spectrum radiation. Goins *et al.* (1997) demonstrated that *Triticum aestivum* plants, grown under RR-emitting diodes, showed significantly lower shoot dry mass than "white light"-(WL) grown *T. aestivum* plants. Moreover, BR and RR exerted specific morphogenetic effects on plants (Smith 1982). Plants demonstrated a shade-avoidance response when grown under BR by increasing stem elongation at the expense of leaf development (Casal and Alvarez 1988, Maas *et al.* 1995). In *Phaseolus vulgaris*, BR stimulated stem elongation and increased dry mass partitioning into stem, at the expense of leaf growth (Maas *et al.* 1995). In *Lolium multiflorum* the BR treatment resulted in reduced leaf growth (Casal and Alvarez 1988). The RR-grown *Pinus nigra* leaves exhibited significantly lower chlorophyll (Chl) *a/b* ratio than that of leaves grown under BR (Milivojević and Tyszkiewicz 1992).

Although chemical growth regulators have been usually used to control plant morphology in many greenhouse crops, research tries to find environment-friendly means, such as spectral filters, for regulating plant growth and morphology (McMahon and Kelly 1995, Rajapakse and Kelly 1995, Kambalapally and Rajapakse 1998). For example, the effects of spectrally filtered sunlight on leaf pigments and morphology of *Chrysanthemum morifolium* were studied by McMahon and Kelly (1995). Radiation was filtered by water (control), which did not absorb solar radiation between 400 and 800 nm, a solution of $CuSO_4$, which absorbed primarily FR, and a blue dye solution, which absorbed primarily RR. Leaves grown under $CuSO_4$-filtered radiation exhibited higher Chl *a*, Chl *b*, and total carotenoid contents per unit area and per dry mass than leaves of plants in control treatment. In addition, leaf anatomy of plants grown under $CuSO_4$ filters resembled that of leaves from plants treated with the chemical growth regulator, daminozide. The blue dye solution-filtered radiation did not influence leaf pigments or morphology compared with control plants. Rajapakse and Kelly (1995) used 6 % $CuSO_4$ and water (control) as spectral filters for testing the effects of radiation quality on growth and saccharide content of *C. morifolium* plants. Radiation transmitted through the $CuSO_4$ filters significantly reduced plant height and internode length compared to control. Application of this kind of radiation resulted in reduced sucrose, glucose, fructose, and starch contents of leaves and stems. Thus filters with specific spectral characteristics could be used as alternative means of producing compact plants in the greenhouses. Kambalapally and Rajapakse (1998) demonstrated that the $CuSO_4$ filtered-radiation significantly reduced plant height and internode length of *Lilium longiflorum*. Therefore, spectral filters are effective for modification of plant growth, and they could be used as an alternative for chemical plant growth regulators in the production of ornamental crops (McMahon and Kelly 1995).

A. mangium Wild. is an important tropical pioneer species, in both economical and ecological terms. Leaves of *A. mangium* develop in two stages. True (compound) leaves are produced during the early development of seedlings; these are later replaced by phyllodes [expanded petioles that form simple, photosynthesising laminae (Esau 1965)] in older plants. Pigment contents and growth characteristics of this plant species depend on irradiance (Yu and Ong 2001). To check the effect of radiation quality on photosynthetic performance and seedling establishment, the photosynthetic radiation-response curves of CO_2 assimilation, Chl contents and fluorescence, and biomass accumulation and allocation of 36 d-old *A. mangium* seedlings grown under WL, BR, RR, and yellow radiation (YR) were used.

Materials and methods

Plants: Seeds of *A. mangium* were collected from Hainan Province, P.R. China. Seeds were pre-treated by immersing in boiling water for 30 s and then soaked in cold water (4 °C) for 24 h. Three pre-treated seeds were sown in each pot (14 cm diameter, 10.8 cm depth) filled with vermiculite (7 cm in depth) and covered with a phytatray. Seeds were germinated and seedlings grown in the teaching garden in the Department of Biological Sciences, National University of Singapore. Plants were kept well watered and were fertilised twice a week with Hoagland's solution. Air temperature was 31±7 °C. Relative humidity of the air ranged from 70 to 100 %.

Radiation quality was varied using phytatrays (*Colored Plastic Phytotram*^{TM}, 114×86×102 mm, *Sigma*, USA), made from clear polystyrene k-resin. Differently coloured phytatrays allowed different wavelengths of radiation to pass through. BR phytatrays (transmission peak at 475 nm, no significant transmission above 550 nm), RR phytatrays (transmission peak at 660 nm, transmit above 590 nm), and YR phytatrays (transmission peak at 580 nm, transmit above 480 nm) were used. In addition, the complete spectrum of sunlight was maintained by allowing radiation to filter through WL phytatrays. All these phytatrays were placed in the garden, with the sun as the sole radiation source. The coloured phytatrays significantly attenuated the photosynthetic photon flux density (PPFD). PPFD of the plants grown under complete spectrum of sunlight (WL phytatrays) was maintained in the same range as all the monochromatic treatments (RR, BR, YR). A quantum sensor (*Li-185b*, *LI-COR*, Lincoln, NB, USA) was used to measure daily fluctuations in PPFD under the differently coloured phytatrays, with the sensor placed beneath the cover of each phytatray. For the daily PPFD experienced by seedlings covered with different phytatrays see Fig. 1.

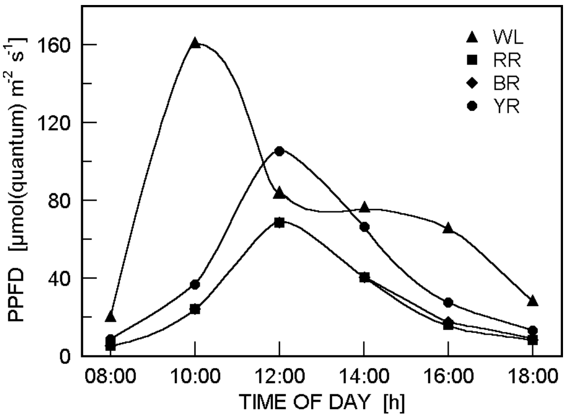

Fig. 1. Daily radiation availability of *A. mangium* seedlings grown in “white light” (WL) or under red (RR), blue (BR), or yellow (YR) monochromatic radiation.

Seed germination lasted 12 d; the number of germinated seeds (out of 60) was counted 8 and 12 d after the seeds were sown.

Chl content, Chl fluorescence, and gas exchange were determined in true (compound) leaves of *A. mangium* 36 d after sowing according to Yu and Ong (2000). Water use efficiency (WUE) was calculated as the ratio of leaf net photosynthetic rate (P_N) to leaf transpiration rate (E) (Farquhar and Richards 1984).

Growth analysis: On day 36 after sowing, seedlings were carefully removed from the pots. Each seedling was divided into several portions (cotyledons, leaf blades, stem plus petioles, and roots). To measure the total leaf area of each seedling, the outlines of the leaflets were drawn on a graph paper. Leaf area was calculated according to an area-mass calibration curve. After determining the fresh mass of different parts of seedlings, plant materials were dried in the oven at 80 °C for 7 d until dry mass was constant, and re-weighed. To obtain the mean mass of a non-germinated seed, seed mass was determined after the removal of the seed coat. The root to shoot ratio (R/S) [dry mass units], specific leaf area (SLA), cotyledon mass ratio (CMR), leaf mass ratio (LMR), stem mass ratio (SMR), root mass ratio (RMR), and leaf area ratio (LAR) were calculated. Relative growth rate (RGR) of each seedling was calculated as: RGR = [ln(seedling mass on day 36) – ln(seed mass)]/36 d (Hunt 1978), where ln = natural logarithm.

Statistics: All experiments were conducted twice, each time with 3 replicates. Each result is presented as the mean ± standard error (SE) of the total number of replicates used. Multiple analysis of variance (Tukey test, $p \leq 0.05$, $n = 6$) was also done.

Results

Seed germination: *A. mangium* is a small-seeded pioneer species. The average mass of each *A. mangium* seed was 12 mg; seed mass became 5.8 mg with the removal of the seed coat. Average length and breadth of *A. mangium* seeds were 2 and 3 mm, respectively. Eight days after sowing, the percentage of seed germination was highest (53 %) in BR; this was followed by the seeds sown and kept in RR (38 %) (Table 1). Twelve days after sowing, the highest germination percentage was still observed in the seeds kept under BR (72 %) and the lowest was observed in YR (48 %) (Table 1). Percentage of seeds germinated under WL was 60 % (Table 1). Seedling survival was also affected by the treatment. The percentage of seedlings that survived in WL, RR, and BR 36 d after sowing ranged between 88–94 % (Table 1). Seedlings grown under YR showed the lowest percentage of survival (38 %) (Table 1).

Table 1. Percent of seed germination and seedling survival of *A. mangium* grown under “white light” (WL) or under red (RR), blue (BR), or yellow (YR) radiation.

Treatment	Germination [%] 8 d after sowing	12 d after sowing	Survival [%] 12 d after sowing
WL	26	60	88
RR	38	63	94
BR	53	72	90
YR	30	48	38

Pigments: The highest Chl (a+b) content was observed in seedlings grown in WL, followed by seedlings grown in RR, YR, and BR (Table 2). The ratio of Chl (a+b)/carotenoids was highest in seedlings grown under WL, and lowest in the seedlings grown in YR (Table 2). The Chl a/b ratio of seedlings grown in BR was significantly higher than that of seedlings grown under RR (Table 2).

Chl fluorescence: The potential photochemical efficiency of photosystem 2 (PS2) under dark-adaptation (F_v/F_m) was 0.81–0.83 for all seedlings (Table 2). Significantly higher values of effective PS2 efficiency under

Table 2. Chlorophyll (Chl) contents [mg m^{-2}], Chl *a/b* and Chl/carotenoids ratios, and Chl fluorescence parameters of *A. mangium* seedlings grown under "white light" (WL) or under red (RR), blue (BR), or yellow (YR) radiation. Means ± SE, *n* = 6. F_v/F_m = potential photochemical efficiency of PS2 under dark-adapted conditions; $\Delta F/F'_m$ = effective PS2 efficiency under irradiance-adapted conditions; q_P = photochemical quenching; NPQ = non-photochemical quenching *via* xanthophyll cycle. Identical letters within the same column indicate no significant differences between the values ($p \leq 0.05$).

	Chl (*a*+*b*)	Chl *a/b*	Carotenoids	Chl/carot	F_v/F_m	$\Delta F/F'_m$	q_P	NPQ
WL	510.94 ± 20.52^a	2.24 ± 0.04^{ab}	52.20 ± 2.05^a	9.80 ± 0.18^a	0.81 ± 0.00^b	0.61 ± 0.01^a	0.80 ± 0.01^a	0.26 ± 0.02^a
RR	317.52 ± 17.60^b	2.15 ± 0.03^b	42.89 ± 2.09^{ab}	7.38 ± 0.10^b	0.83 ± 0.00^a	0.42 ± 0.01^c	0.54 ± 0.01^c	0.30 ± 0.06^a
BR	284.23 ± 18.71^{bc}	2.30 ± 0.04^a	37.46 ± 2.17^b	7.56 ± 0.18^b	0.81 ± 0.00^b	0.60 ± 0.01^a	0.81 ± 0.01^a	0.37 ± 0.03^a
YR	316.75 ± 20.40^b	2.27 ± 0.03^{ab}	45.02 ± 3.54^{ab}	7.13 ± 0.21^{bc}	0.81 ± 0.00^b	0.53 ± 0.01^b	0.70 ± 0.02^b	0.26 ± 0.03^a

radiation-adapted conditions ($\Delta F/F'_m$) were observed in seedlings grown in BR and WL, and lowest in seedlings grown in RR (Table 2). Changes in photochemical quenching (q_P, proportion of open PS2) of seedlings grown in different treatments showed the same pattern as the changes in $\Delta F/F'_m$ (Table 2). Non-photochemical quenching (NPQ), linearly related to thermal energy dissipation, was not significantly different in seedlings grown under the different radiation treatments (Table 2).

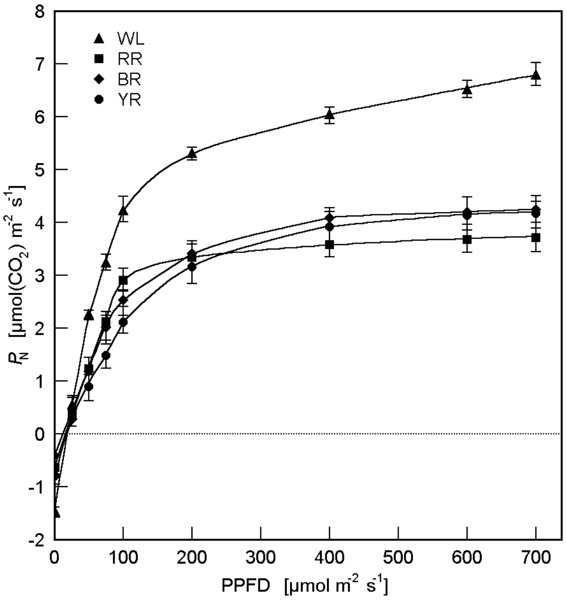

Fig. 2. Typical photosynthetic irradiance-response curves of *A. mangium* seedlings grown under "white light" (WL) or under red (RR), blue (BR), or yellow (YR) radiation. Error bars indicate SE (*n* = 6).

Gas exchange: Seedlings grown under WL exhibited significantly higher maximal P_N than those grown under RR, BR, and YR (Fig. 2). No significant differences in P_N of seedlings grown under RR, BR, and YR were found (Table 3). Dark respiration rate (R_D) and apparent quantum yield (Φ) did not differ significantly among the seedlings grown under monochromatic radiation (Table 3), but they were significantly lower than that of the plants grown under WL. No significant differences in stomatal conductance (g_s) among seedlings grown under all treatments were found (Table 3). *E* was highest in plants grown under WL, and lowest in plants grown under monochromatic radiation (Table 3). No significant difference in compensation irradiance amongst WL, BR, RR, and YR seedlings was found. The saturation irradiance of WS seedlings was 201 μmol m^{-2} s^{-1}, and the lowest value of LSP was observed in seedlings grown under RR and BR (Table 3). There was no significant difference in WUE among the seedlings grown in any of the treatments (Table 3).

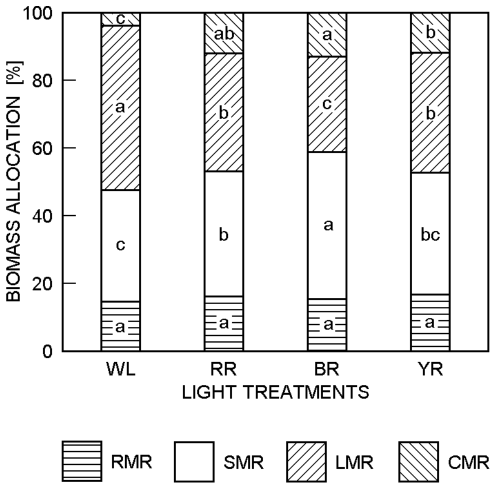

Fig. 3. The proportion of biomass allocated to cotyledons, leaves, stems and petioles, and roots in *A. mangium* seedlings grown under "white light" (WL) or under red (RR), blue (BR), or yellow (YR) radiation. CMR = cotyledon mass ratio; LMR = leaf mass ratio; SMR = stem mass ratio; RMR = root mass ratio.

Growth and biomass allocation: Total dry mass and total leaf area of seedlings grown in monochromatic radiation (RR, BR, and YR) were significantly lower than in seedlings grown in WL. SLA was, however, significantly higher in BR, RR, and YR grown seedlings (Table 4). The LAR of RR seedlings was the highest (Table 4).

Fig. 3 shows the proportion of total plant biomass allocated to cotyledons, leaves, stems, and roots in *A. mangium* seedlings grown under all treatments. No difference

Table 3. Changes in maximal rate of net photosynthetic CO_2 uptake (P_N) [μmol(CO_2) m^{-2} s^{-1}], apparent quantum yield (Φ) [mol(CO_2) mol^{-1}(quantum)], dark respiration rate (R_D) [μmol(CO_2) m^{-2} s^{-1}], stomatal conductance (g_s) [mmol(H_2O) m^{-2} s^{-1}], transpiration rate (*E*) [mmol(H_2O) m^{-2} s^{-1}], compensation irradiance (CI) [μmol(quantum) m^{-2} s^{-1}], saturation irradiance (SI) [μmol(quantum) m^{-2} s^{-1}], and water use efficiency (WUE) [mmol(CO_2) mol^{-1}(H_2O)] of *A. mangium* leaves grown under WL, RR, BR, and YR. The latter three parameters were determined at 700 μmol(quantum) m^{-2} s^{-1}. Means ± SE, *n* = 6. Identical letters within the same column indicate no significant difference between the values ($p \leq 0.05$).

	P_N	Φ	R_D	g_s	*E*	CI	SI	WUE
WL	7.03 ± 0.13^a	0.06 ± 0.00^a	1.53 ± 0.11^a	81.33 ± 9.89^a	2.16 ± 0.25^a	19.67 ± 1.22^a	201.67 ± 21.67^a	3.44 ± 0.31^a
RR	3.83 ± 0.36^b	0.03 ± 0.00^b	0.47 ± 0.07^b	72.83 ± 7.74^a	1.48 ± 0.17^a	12.33 ± 1.41^a	130.00 ± 9.66^b	2.64 ± 0.19^a
BR	4.34 ± 0.17^b	0.03 ± 0.00^b	0.58 ± 0.11^b	71.20 ± 9.10^a	1.36 ± 0.19^a	19.20 ± 3.09^a	112.00 ± 4.47^b	3.55 ± 0.55^a
YR	4.30 ± 0.31^b	0.03 ± 0.00^b	0.77 ± 0.12^b	83.67 ± 12.52^a	1.64 ± 0.20^a	20.50 ± 3.79^a	206.67 ± 6.67^a	2.76 ± 0.30^a

in RMR was found. The proportion of biomass allocated to stem (SMR) was significantly higher in BR seedlings than that of seedlings grown under WL, RR, and YR. However, LMR of BR seedlings was significantly lower than that of other seedlings (Fig. 3). The LMR of seedlings grown under WL was significantly higher that in the other groups of seedlings, while cotyledon mass ratio (CMR) of WL seedlings was significantly lower than that of other seedlings (Fig. 3).

Table 4. Growth characteristics of *A. mangium* seedlings grown under WL, RR, BR, and YR. For explanation of symbols see the text. Means ± SE, *n* = 6. Identical letters within the same column indicate no significant differences between the values ($p \leq 0.05$).

	Total DM [g]	RGR [g $kg^{-1}d^{-1}$]	Leaf area [cm^2]	SLA [m^2 kg^{-1}]	LAR [m^2 kg^{-1}]	R/S
WL	36.78 ± 2.32^a	54.60 ± 1.78^a	10.95 ± 0.18^a	62.78 ± 2.97^c	30.35 ± 1.89^b	0.18 ± 0.01^a
RR	9.18 ± 0.45^b	16.17 ± 1.37^b	3.53 ± 0.11^b	112.60 ± 6.27^a	38.77 ± 1.63^a	0.20 ± 0.01^a
BR	8.07 ± 0.75^b	12.14 ± 2.58^b	2.30 ± 0.21^b	103.73 ± 1.80^{ab}	28.58 ± 0.96^b	0.18 ± 0.02^a
YR	9.70 ± 0.58^b	17.63 ± 1.59^b	3.00 ± 0.07^b	88.81 ± 3.76^b	31.35 ± 1.55^b	0.21 ± 0.01^a

Discussion

Germination: Preliminary germination experiments showed that non-pre-treated *A. mangium* seeds, kept in the dark or light, did not germinate at all. Also pre-treated *A. mangium* seeds kept in total darkness did not germinate. Hence radiant energy was an important environmental cue to stimulate seed germination of *A. mangium*. Generally, seed germination of pioneer species is enhanced by fluctuations in environmental factors such as irradiation, temperature, *etc.* (Bazzaz 1996). Small-seeded pioneer species, such as *Piper auritum* and *Cecropia obtusifolia*, commonly need light for germination (Vázquez-Yanes and Smith 1982, Vázquez-Yanes and Orozco-Segovia 1987, Kozlowski *et al.* 1991). Small-seeded pioneer species like *A. mangium* have limited seed reserves; therefore they cannot sustain long-term seedling growth under shade.

The highest germination percentage was observed in *A. mangium* seeds exposed to BR. This indicated that the germination of *A. mangium* seeds would be enhanced under wavelengths that mimick those in forest gaps and along forest fringes. When radiation passes through a canopy, leaves preferentially absorb RR and BR, thus very little BR reaches the forest floor (Tinoco-Ojanguren and Pearcy 1995). The lowest germination percentage and highest seedling mortality were observed in the *A. mangium* seeds and seedlings kept under YR, because YR does not correspond to the absorption spectra of Chls and carotenoids of higher plants; therefore, photosynthesis could not proceed (McCree 1971/2).

Spectral characteristics and growth and photosynthesis: Different morphological responses to different radiation quality were observed in seedlings grown under WL and monochromatic radiation. SLA of monochromatic radiation-grown seedlings was 42–78 % higher than that of WL grown seedlings. In monochromatic radiation, the energy of photons from the RR, BR, and YR regions of the spectrum would be lower than that of WL (Sager *et al.* 1982). To increase photon absorption and to compensate for the lower radiant energy in their growth environments, monochromatic radiation-grown seedlings produced greater SLA.

The biomass accumulation and allocation patterns of *A. mangium* seedlings grown under WL, BR, RR, and YR were closely linked with their physiological activities. Compared with seedlings grown under WL, in seedlings grown under BR, RR, and YR, P_N, R_D, and apparent quantum yield were about 50 % lower. Lower photon-saturated P_N in monochromatic radiation-grown seedlings observed in this study was consistent with other reports showing that *Triticum aestivum* and *Capsicum annuum* plants grown under red LEDs (light-emitting diodes) exhibited low photon-saturated P_N (Brown *et al.* 1995, Goins *et al.* 1997). This could be the result of the narrow transmission peaks of BR, RR, and YR, leading to an imbalance of photons available to PS1 and PS2 and thus changing the ratio of cyclic to whole chain electron transport (Tennessen *et al.* 1994). Moreover, utilisation efficiency of photons from the narrow red, blue, and yellow regions of spectrum by plants for photosynthesis would be lower than that of full spectrum radiation (Sager *et al.* 1982). The lower R_D in monochromatic radiation-grown seedlings, relative to WL-grown seedlings, suggested that the metabolic activities in these seedlings were low. Values of CI in BR, RR, and YR grown seedlings were also low. These responses were advantageous adaptations for seedlings grown under such conditions, as they aided the seedlings to maintain a positive carbon balance under the monochromatic radiation. Lower apparent quantum yield of monochromatic radiation-grown seedlings indicated that the efficiency of photon utilisation during photosynthesis was lower in monochromatic radiation-grown seedlings than in WL seedlings. g_s and WUE of seedlings grown under monochromatic radiation were similar to those of WL seedlings showing that these two physiological parameters were not affected by radiation quality. Thus g_s and CO_2 availability did not limit photosynthesis in the *A. mangium* seedlings grown under BR, RR, and YR.

RGR of monochromatic radiation-grown seedlings was only 20–25 % of that of WL-grown seedlings. The lower RGR in the monochromatic radiation-grown seedlings could, probably, be attributed to their low physiological activities. Photon-saturated P_N and R_D of monochromatic radiation-grown seedlings were significantly lower than those of WL-seedlings.

Different radiation quality did not affect the potential quantum yield of PS2 (F_v/F_m) of *A. mangium* seedlings. A similar result was reported in the red alga, *Porphyra leucosticta* (Aguilera et al. 2000). Compared with that of seedlings grown under RR and YR, the effective quantum yield of PS2 ($\Delta F/F'_m$) and the fraction of open PS2 reaction centres (q_P) were significantly higher in BR seedlings. Hence BR, a probable signal for plants adapted to open sites, was more crucial than RR and YR for the efficient functioning of PS2 in *A. mangium* seedlings. Because $\Delta F/F'_m$ is directly related to photosynthetic non-cyclic electron transport (Schreiber *et al.* 1994), the photosynthetic non-cyclic electron transport rate was higher in seedlings grown under BR than that of seedlings grown under RR and YR. Lower $\Delta F/F'_m$ in leaves of RR and YR plants indicated a down-regulation of non-cyclic electron transport, most probably a result of lower PPFD and narrow transmission peaks of the different monochromatic wavelengths, leading to a reduction in Calvin cycle activities. Thus, the relatively low q_P observed in RR and YR leaves, indicating higher excitation pressure in PS2 of these plants, suggested that some reaction centres were closed and that the proportion of absorbed energy utilised by photosynthesis in these seedlings was low. All these results show that different radiation quality resulted in altered efficiency of PS2 of the leaves of *A. mangium* seedlings, in terms of photon absorption and transduction. This might be the result of different spectral energy distribution in BR, RR, and YR, as BR had higher energy per photon than RR.

Different spectral characteristics modulated distinct morphological responses in *A. mangium* seedlings. BR stimulated shade-avoidance responses of *A. mangium* seedlings, and RR induced shade-tolerant reactions of *A. mangium* seedlings. The high SMR and low LMR observed in BR seedlings indicated they invested more biomass into stem growth at the expense of photosynthetic structures (leaves). This observation was consistent with other studies reporting that BR evokes plant responses analogous to shade-avoidance reactions (Casal and Alvarez 1988, Maas *et al.* 1995). For example, BR-grown *Phaseolus vulgaris* plants exhibited increased stem elongation and increased dry mass partitioning into stem, compared with the plants under full spectrum (Maas *et al.* 1995). Shade avoiders, generally, tend to redirect their development in low irradiance to favour stem extension at the expense of leaf development (Smith 1982). However, to increase both the relative amount of photons captured and the efficiency of photon capture under low irradiance, shade-tolerant plants, generally, invest a greater part of their biomass into photosynthetic structures but not into stem growth (Smith 1982). In this study, the *A. mangium* seedlings grown under RR also exhibited a shade-tolerant syndrome. They displayed significantly higher LAR and lower SMR than the seedlings grown under BR.

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