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Photosynthetic characteristics, dark respiration, and leaf mass per unit area in seedlings of four tropical tree species grown under three irradiances

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Abstract

We investigated the effect of growth irradiance (I) on photon-saturated photosynthetic rate ($P_{\max}$), dark respiration rate (R_D), carboxylation efficiency (CE), and leaf mass per unit area (LMA) in seedlings of the following four tropical tree species with contrasting shade-tolerance. *Anthocephalus chinensis* (Rubiaceae) and *Linociera insignis* (Oleaceae) are light-demanding, *Barringtonia macrostachya* (Lecythidaceae) and *Calophyllum polyanthum* (Clusiaceae) are shade-tolerant. Their seedlings were pot-planted under shading nets with 8, 25, and 50 % daylight for five months. With increase of I, all species displayed the trends of increases of LMA, photosynthetic saturation irradiance, and chlorophyll-based $P_{\max}$, and decreases of chlorophyll (Chl) content on both area and mass bases, and mass-based $P_{\max}$, R_D, and CE. The area-based $P_{\max}$ and CE increased with I for the light-demanders only. Three of the four species significantly increased Chl-based CE with I. This indicated the increase of nitrogen (N) allocation to carboxylation enzyme relative to Chl with I. Compared to the two shade-tolerants, under the same I, the two light-demanders had greater area- and Chl-based $P_{\max}$, photosynthetic saturation irradiance, lower Chl content per unit area, and greater plasticity in LMA and area- or Chl-based $P_{\max}$. Our results support the hypothesis that light-demanding species is more plastic in leaf morphology and physiology than shade-tolerant species, and acclimation to I of tropical seedlings is more associated with leaf morphological adjustment relative to physiology. Leaf nitrogen partitioning between photosynthetic enzymes and Chl also play a role in the acclimation to I.

Additional key words: acclimation to irradiance; *Anthocephalus*; *Barringtonia*; *Calophyllum*; carboxylation efficiency; chlorophyll; leaf mass per unit area; *Linociera*; net photosynthetic rate; nitrogen.

Introduction

Forest environment is very heterogeneous in both space and time (Oldeman 1990, Oliver and Larson 1990). The highly heterogeneous environments within forests allow plants of different ecological groups to find proper sites to establish themselves and to coexist within the forests (Grubb 1977). In forests, irradiance (I) is the most important factor that affects regeneration and growth of forest trees (Oldeman 1990, Oliver and Larson 1990). Light-demanding species require high I sites such as canopy gaps for successful regeneration (Whitmore 1989). Some shade-tolerant species can regenerate in both sunny and shady sites, while some extreme shade-tolerant species can only regenerate in shady sites. The temporal change of I within forests requires the morphological and physiological responses of forest plants. Light-demanding species are more flexible in both morphology and physiology in response to environmental change, compared to extreme shade species (Boardman 1977, Chazdon *et al.* 1996, Valladares *et al.* 2000).

To grow in low I habitats such as forest understorey, where plants have a low carbon gain, they must minimize carbon loss through reduction of both respiration and construction cost of supporting *vs.* assimilation tissues (Givnish 1988), and to have a high efficiency of photon capture through achieving a high content of chlorophyll (Chl). Leaf dark respiration rate (R_D) per unit area usually increases with plant growth I (Lusk and Reich 2000). Leaf mass per unit area (LMA) that is related to leaf thickness and density also increases with I for most of broadleaved trees, resulting in lower construction cost per

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unit leaf area and lower leaf maintenance cost in lower *I*. Also, LMA is closely correlated with several leaf physiological traits such as PPFD (photosynthetic photon flux density) saturated photosynthetic rate and R_D (Reich *et al.* 1997, Mitchell *et al.* 1999). Leaf Chl content per unit mass decreases with increase of *I* (Lee *et al.* 1990, Cao 2000). In addition, plant acclimation to *I* may involve the different leaf nitrogen (N) partitioning to assimilation enzymes relative to Chl (Rosati *et al.* 1999, Le Roux *et al.* 2001).

Tropical rain forests are increasingly suffering from deforestation and other nature or human interferences (FAO 1993, Nepstad *et al.* 1999). To conserve and manage the remaining forests and to restore or afforest the degraded forestlands, there are urgent needs on knowledge of the forest trees' ecology and physiology, particularly in the regions where such knowledge is very limited. This study was aimed (*1*) to clarify the photosynthetic characteristics of four tropical rain forest species and *I* effect on their photosynthetic physiology, (*2*) to test whether light-demanding species have greater phenotypic plasticity than shade-tolerant species.

Materials and methods

This study was carried out in the Xishuangbanna Tropical Botanical Garden (21°56'N, 101°15'E, 600 m altitude), Chinese Academy of Sciences, which is situated in the southern part of Yunnan Province, South-west China. Here, the mean annual temperature is 21.7 °C; mean temperature of the hottest month (July) is 25.3 °C and 15.6 °C of the coolest month January (Liu and Li 1996, Cao and Zhang 1997). The minimum temperature recorded was 2 °C. Mean annual precipitation was about 1 560 mm. Due to the pronounced influence of the summer monsoons that come from the Bay of Bengal, about 83 % of the annual rainfall concentrates in the period from May to October. The period from November to April is short of rainfall. However, from November to February, there is a heavy fog almost every day from midnight to around next midday. The fog contributes significantly to maintain the moistures of both air and soil.

Various formations of tropical forests flourish in the region of southern Yunnan, such as wet riparian rain forests, seasonal rain forests, and montane rain forests, and seasonal rain forests on limestone hills (Wu 1987, Cao and Zhang 1997, Zhu 1997). The physiognomy and plant species richness of these forests resemble the tropical rain forests in Southeast Asia (Cao and Zhang 1997, Zhu 1997). Four tropical rain forest tree species as introduced below were included in this study. *Anthocephalus chinensis* (Lam.) Rich. *ex* Walp. (Rubiaceae) is a pioneer tree, and an important timber species used for plantation in this region. *Linociera insignis* C.B. Clarke (Oleaceae) is a sub-canopy tree that requires canopy gaps and forest edge environment for regeneration. *Calophyllum polyanthum* Wall. *ex* Choisy (Clusiaceae) is a climax canopy tree that is able to regenerate in forest understorey. *Barringtonia macrostachya* (Jack) Kurz (Lecythidaceae) is very shade-tolerant, lower storey species. In May 2000, seedlings germinated from seeds of the four species were nursed in the nursery. After two months, when the seedlings had more than two leaves, they were transplanted into pots (15 000 cm^3), one seedling per pot. The pots contained forest soil of upper 10 cm layer. The potted seedlings were grown under shading nets supplying *I* of 8, 25, and 50 % daylight, respectively. The relative *I* values under the three shade plots were estimated with integrated PPFD under the shade plots over a clear day in the summer compared with that in a fully open site. The PPFD was measured with *Li-190SA* quantum sensors and recorded with a *Li-1400* data logger (*Li-Cor*, USA). The *I* close to that of forest understorey was not used in this study because the seedlings of the pioneer tree cannot grow well under this *I*. The potted seedlings were watered everyday, and were regularly fertilized and checked regularly for weeds, insects, and diseases. In December 2000, using an open photosynthetic system of *Li-6400* (*Li-Cor*, USA), photosynthetic *I* responses were measured for three to five fully expanded leaves (one leaf per plant) of each species under each of the three *I*. Using 9 doses of PPFD, *i.e.* 2 000, 1 500, 1 000, 500, 200, 100, 50, 20, and 0 µmol m^{-2} s^{-1}, and starting from the highest PPFD, net photosynthetic rate (P_N) under each PPFD was measured when the leaf was irradiated for 3 min. Air conditions in the leaf chamber were controlled, with air speed of 8.33 cm^3 s^{-1}, CO$_2$ concentration of 360 µmol mol^{-1}, air temperature of 25 °C, relative humidity of 50 %, and water vapour pressure of 1.58 kPa. Prior to this experiment, the leaf was placed under an artificial "cold light" for 30 min in order to achieve the leaf's fully photosynthetic induction. This "cold light" was provided by several lamps hanging above a glass water bath with flowing tap water in it. Different irradiances were used for photosynthetic induction for different species from different growth *I*, with a range between 600–1 200 µmol m^{-2} s^{-1}. These photosynthetic measurements were done between 08:30 and 11:30. Photosynthetic irradiance response curves were fitted with the following equation (Zhang and Xu 2000):

$$P_N = P_{max}\,(1 - C_0\,e^{-\alpha\,PPFD/P_{max}})$$

where P_{max} is the maximum P_N, α is quantum yield under low PPFD, and C_0 is the dimensionless coefficient when P_N approaches zero under low PPFD. If the fitness test of the equation is satisfied, the photosynthetic compensation irradiance (I_{comp}) is calculated as:

$$I_{comp} = P_{max}\,\ln(C_0)/\alpha.$$

When P_N approaches 99 % of P_{max}, PPFD is assumed as the photosynthetic saturation irradiance (I_{sat}) and is calculated as:

$I_{sat} = P_{max} \ln(100\ C_0)/\alpha$

Photosynthetic CO_2 responses were measured with CO_2 concentrations ranging from 0 and 360 μmol mol^{-1}, using the control CO_2 system of the machine to regulate CO_2 concentration in the leaf chamber, and a LED source providing a PPFD that is based on I_{sat} of a species under a given I. P_N was measured when leaves were stabilized at each CO_2 concentration for about 1 min. The slope of the linear regression of intercellular CO_2 concentration and P_N at the low CO_2 concentration is the carboxylation efficiency (CE) (Cai and Xu 2000). Placing leaves in dark for 2 min, R_D was measured with the photosynthetic system. According to Arnon (1949), leaf Chl content on the bases of both leaf area (Chl_{area}) and dry mass (Chl_{mass}) was determined for the leaves used for photosynthetic measurement. Using a punch, five leaf discs from a sample leaf were taken, treated in an oven under 120 °C for 30 min, and then dried in the oven under 80 °C for 24 h. The leaf mass per unit area (LMA) was determined for three to five leaves of each species under each I. The P_{max}, CE, and R_D were expressed on the bases of both leaf area ($P_{max\text{-}area,}$ CE_{area}, and $R_{D\text{-}area}$) and leaf dry mass ($P_{max\text{-}mass}$, CE_{mass}, and $R_{D\text{-}mass}$), respectively. The rates based on leaf area are related to leaf morphology and tissue chemical properties, while those based on leaf dry mass are related to leaf chemical and assimilation properties. The plasticity index was calculated for some physiological and leaf traits (Table 2) under the three I as (Valladares *et al.* 2000): (maximum – minimum)/maximum.

Significance of differences among means of physiological and leaf traits under the three I were analysed for each species using *ANOVA*. The relationship of $P_{max,}$, CE*,* R_D, and Chl on the basis of leaf mass with LMA was analyzed using power functions.

Results

With increase of I, all species displayed the trends of increases of LMA and $P_{max\text{-}Chl}$, while Chl contents on both area (Chl_{area}) and mass bases (Chl_{mass}), and mass-based P_{max}, R_D, and CE declined (Fig. 1, Table 1). $P_{max\text{-}mass}$ tended to increase with I for the two light-demanding species only (Fig. 1*A, D*). Both CE_{area} and CE_{Chl} increased with I for all species except for *B. macrostachya* (Fig. 1*D, F*). Increase of CE_{Chl} with I revealed higher proportion of leaf N allocation to photosynthetic enzyme relative to Chl.

Among species, *A. chinensis* had the smallest LMA, while *C. polyanthum* had the largest LMA (Table 1). Both $P_{max\text{-}area}$ and $P_{max\text{-}Chl}$ followed the order: *A. chinensis* > *L. insignis* > *B. macrostachya* > *C. polyanthum* (Fig. 1*A–C*); some of the differences between the two shade-tolerant species were non-significant. Under the same I, *A. chinensis* had the largest and *B. macrostachya* the smallest $R_{D\text{-}area}$ (Table 1). For each of the four species, $R_{D\text{-}area}$ between seedlings grown under 8 and 25 % daylight were not significantly different, but they were significantly smaller than those in seedlings grown under 50 % daylight.

The two light-demanding species had higher CE_{area} and CE_{Chl} values than the two shade-tolerant species (Fig. 1*D–F*). Between the two ecological groups, the difference in CE_{Chl} was more pronounced than that in CE_{area}. Among species, under the same I, *A. chinensis* had the largest CE_{area} and CE_{Chl} values.

The light-demanders tended to have greater I_{sat} than the shade-tolerants, with the largest value for *A. chinensis* and the smallest one for *C. polyanthum* (Table 1). Under the 8 % daylight, this difference between the two groups was less pronounced. Under both 8 and 50 % of daylight, I_{comp} values were not significantly different among species (Table 1) while in 25 % daylight, I_{comp} of the light-demanders were significantly greater than those of the shade-tolerants. For all species, their I_{comp} in 50 % daylight were significantly greater than those in 8 % daylight for the same species.

Under the 50 % daylight, Chl_{area} was not significantly different among species (Table 1), while under both 8 and 25 % daylight, the two light-demanding species had significantly lower Chl_{area} than the two shade-tolerant species. Under the same I, Chl *a*/*b* ratios were similar among species. For all species, Chl *a*/*b* under 8 % daylight was significantly smaller than under 50 % daylight for the same species.

Using the pooled data of the mean values of each of the four species under the three I, $P_{max\text{-}mass,}$ CE_{mass}, $R_{D\text{-}mass}$, and Chl_{mass} were strongly related to LMA in the fashion of power functions (Fig. 2).

Table 2 shows the phenotypic plasticity indices of eleven physiological and morphological traits of the four species. For most of the eleven traits, with few exceptions such as I_{comp} and Chl_{area}, the two light-demanding species had greater phenotypic plasticity than the two shade-tolerant species.

Discussion

The larger phenotypic plasticity of the two light-demanding species compared to the two climax shade-tolerant species (Table 2) is consistent with specialization-plasticity hypothesis (Lortie and Aarssen 1996). This hypothesis predicts that specialization in favourable environments increases plasticity, whereas specialization in less favourable environments decreases the plasticity. Both *B. macrostachya* and *C. polyanthum* that require

Table 1. Leaf mass per unit area (LMA), dark respiration rates in terms of leaf area ($R_{\text{D-area}}$) and mass ($R_{\text{D-mass}}$), photosynthetic saturation irradiance (I_{sat}) and compensation irradiance (I_{comp}), chlorophyll content per unit leaf area (Chl_{area}) and mass (Chl_{mass}), and Chl *a/b* for the four tropical tree species grown under the three irradiances. Means ± standard errors (n = 3–5). *Different upper- and lower-case letters* indicate significant differences in the means of the same species under three different irradiances and in those of different species under the same irradiances (p<0.05, *ANOVA*), respectively.

Parameters	I [%]	*Anthocephalus*	*Linociera*	*Barringtonia*	*Calophyllum*
LMA [g m^{-2}]	50	56.1±2.3Ac	110.2±0.7Aa	79.1±2.8Ab	110.3±4.1Aa
	25	37.7±2.5Bc	75.9±3.5Ba	55.9±0.5Bb	81.1±1.3Ba
	8	23.6±1.2Cc	50.1±0.8Cb	48.7±0.3Cb	74.9±6.1Ba
$R_{\text{D-area}}$ [µmol m^{-2} s^{-1}]	50	1.31±0.07Aa	0.96±0.05Ab	0.72±0.02Ac	0.94±0.06Ab
	25	0.99±0.07Ba	0.79±0.03Bb	0.62±0.02Bc	0.74±0.03Bb
	8	0.91±0.02Ca	0.79±0.03Bb	0.57±0.02Cb	0.73±0.02Bb
$R_{\text{D-mass}}$ [µmol kg^{-1} s^{-1}]	50	23.39±1.23Ac	8.67± 0.40Ab	9.47±0.25Ab	8.54±0.50Aa
	25	26.28±1.81Ac	10.44±0.34Bab	11.01±0.30Bb	9.17±0.31Aa
	8	38.49±0.86Bc	15.77 ± 0.52Cb	11.73±0.44Bd	9.65±0.21Aa
I_{sat} [µmol m^{-2} s^{-1}]	50	1570.0±95.8Aa	1151.2±71.8Ab	1026.0±80.3Ac	594.5±43.5Ad
	25	635.6±9.5Ba	572.3±49.4Bab	609.5±92.9Bab	448.9±28.5Bb
	8	661.9±66.9Ba	444.6±30.3Bb	407.4±50.4Bb	371.3±33.9Bb
I_{comp} [µmol m^{-2} s^{-1}]	50	12.7±0.9Aa	13.6±1.0Aa	15.2±1.6Aa	13.6±1.6Aa
	25	12.8±1.2ABa	13.7±1.3ABa	9.2±1.3ABb	7.6±0.8Bb
	8	7.4±1.3Ba	8.2±1.3Ba	6.70±1.0Ba	8.2±1.0Ba
Chl_{area} [mmol m^{-2}]	50	0.23±0.02Aa	0.23±0.01Aa	0.31±0.04Aa	0.29±0.03Aa
	25	0.34±0.02ABa	0.31±0.02Ba	0.39±0.02Ab	0.52±0.04Bc
	8	0.38±0.02Ba	0.47±0.01Ca	0.58±0.04Bb	0.60±0.03Bb
Chl_{mass} [mmol kg^{-1}]	50	4.17± 0.33Ac	2.06 ± 0.07Aa	3.96±0.47Acb	2.60±0.27Aab
	25	8.97± 0.55Bc	4.14 ± 0.19Bb	7.07±0.40Ba	6.39±0.50Ba
	8	16.01± 0.65Cb	9.29 ± 0.13Ca	11.93±0.79Cc	8.08±0.44Ba
Chl *a*/*b*	50	2.60±0.05Aa	2.44±0.06Aa	2.48±0.11Aa	2.59±0.02Aa
	25	2.50±0.07Aa	2.48±0.04Aa	2.55±0.15Aa	2.45±0.03Ba
	8	2.08±0.10Ba	1.64±0.18Ba	1.88±0.13Ba	2.44±0.05Bb

the unfavourable forest understorey sites for regeneration had lower physiological and morphological plasticity. The large plasticity of the pioneer and gap species also supports the idea that predictability of environmental heterogeneity determines the direction of evolutionary changes in phenotypic plasticity (Scheiner 1993). Pioneer and light-demanding species spend most of their lives in the habitats such as in early succession plant communities or forest canopy gaps, where environmental progression is relatively predictable. In contrast, most of climax canopy species or lower storey species experience once or several times an abrupt environmental change such as canopy gap formation during their ontogeny from seedlings to mature trees (Canham 1990, Cao and Ohkubo 1999). This change of environment is largely dependent on chance and is thus unpredictable (Lorimer and Frelich 1988). Therefore, plasticity in climax species may be not favoured by selection (Valladares *et al.* 2000).

Leaf N partitioning between photosynthetic enzymes and Chl is an important component in plant physiological acclimation to different I (Le Roux *et al.* 2001, Warren and Adams 2001). All the studied species displayed increase of CE_{area} with I (Fig. 1), indicating increase of photosynthetic enzyme activity per unit leaf area. Moreover, their CE_{chl} increased with I (Fig. 1). This revealed higher allocation ratio of leaf N to photosynthetic enzymes relative to Chl. For the two light-demanding species increases of both CE_{area} and CE_{chl} in high I were consistent with the increase of $P_{\text{max-area}}$ (Fig. 1). However, for the two shade-tolerant species $P_{\text{max-area}}$ lacked acclimation in spite of variation of CE_{area} and CE_{chl} with I. The reason for this later case is not clear. On the other hand, however, relatively stable and low $P_{\text{max-area}}$ as reported for the two shade-tolerant species studied are consistent with the reports for other extreme shade-tolerant plants (Boardman 1977, Chazdon *et al.* 1996). Both increase

Table 2. Phenotypic plasticity indices for each of the eleven structural and physiological parameters of the four tropical rainforest species grown in the three irradiances. Explanations of the calculation and abbreviations of parameters are given in the text.

Parameter	*Anthocephalus*	*Linociera*	*Barringtonia*	*Calophyllum*
LMA	0.579	0.546	0.385	0.321
$P_{\text{max-area}}$	0.401	0.419	0.024	0.053
$P_{\text{max-Chl}}$	0.631	0.716	0.451	0.518
$R_{\text{D-area}}$	0.307	0.174	0.202	0.233
CE_{area}	0.351	0.257	0.332	0.150
CE_{Chl}	0.598	0.635	0.199	0.608
I_{sat}	0.578	0.614	0.542	0.376
I_{comp}	0.415	0.399	0.558	0.439
Chl_{area}	0.382	0.512	0.461	0.525
Chl_{mass}	0.739	0.778	0.668	0.677
Chl *a/b*	0.199	0.337	0.263	0.057
Mean plasticity	0.471	0.490	0.371	0.360
Standard error	0.049	0.058	0.057	0.065

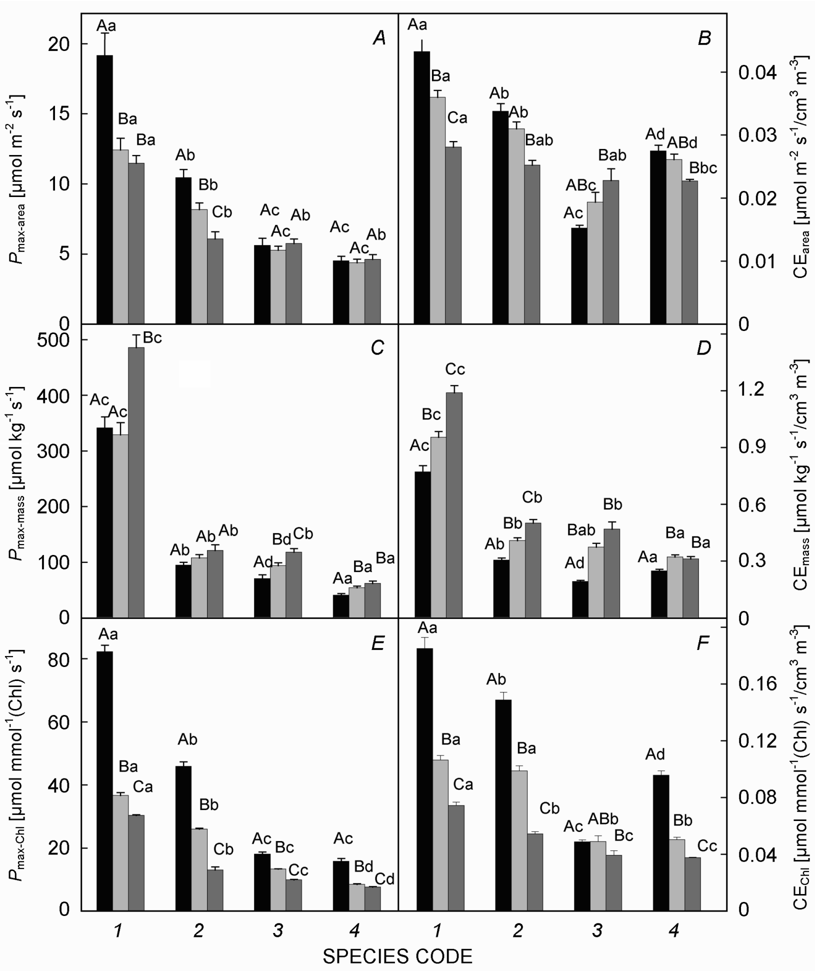

Fig. 1. Maximum photosynthetic rate, $P_{\max}$ (*A, C, E*) and carboxylation efficiency, CE (*B, D, F*) of the four species (*1*, *Anthocephalus chinensis*; *2*, *Linociera insignis*; *3*, *Barringtonia macrostachya*; *4*, *Calophyllum polyanthum*) grown under the growth irradiances of 50 % (*black bars*), 25 % (*light gray bars*), and 8 % daylight (*intermediate gray bars*), respectively. Means ± SE (n = 3–5). *Different upper case and lower case letters* above the bars indicate significant differences in the means of the same species under three irradiances and in those of different species under the same irradiance (p<0.05, *ANOVA*), respectively.

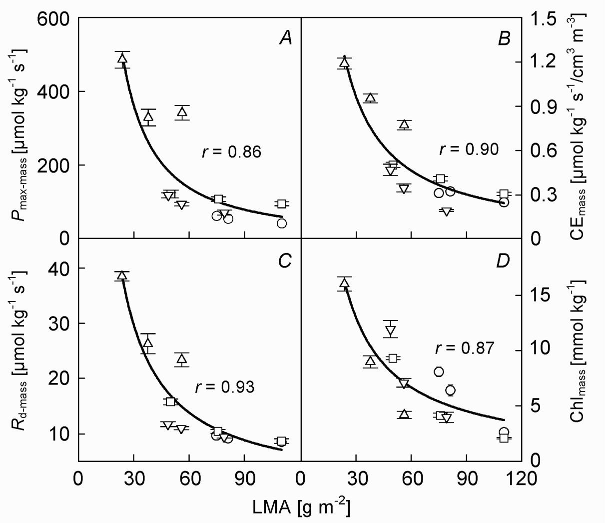

Fig. 2. Maximum photosynthetic rates ($P_{max-mass}$), dark respiration rates (R_{D-mass}), carboxylation efficiency (CE_{mass}), and chlorophyll content (Chl_{mass}) on the basis of leaf mass as a function of leaf mass per unit leaf area (LMA), using the data pooled from the four species (Δ, *Anthocephalus chinensis*; □, *Linociera insignis*; ∇, *Barringtonia macrostachya*; ○, *Calophyllum polyanthum*) grown under the irradiances of 8, 25, and 50 % daylight. Means±SE of one species from one irradiance. Regression lines are fitted with power functions ($p<0.001$).

of R_{D-area} and decrease of Chl content on either mass or area bases with I as found in all studied species (Table 1) are a favourable acclimation. In low I, a low R_{D-area} is beneficial for plants to achieve positive carbon balance (Givnish 1988). An important fraction of R_D is associated with protein turnover (Lambers *et al.* 1983, Ryan 1995). The decreasing R_{D-area} with decreasing I (Table 1) was in agreement with the decreases of both CE_{area} and CE_{Chl} with decrease of I for all studied species except for *B. macrostachya* (Fig. 1). This is consistent with the idea that low metabolic activity is adaptive in low I (Lusk and Reich 2000). Further, Chl is the main site that traps photons. In low I, increase of Chl content (Table 1) helps to enhance plant ability to capture the limited I resources.

With pooled data for the four species from all I, LMA was closely related to mass-based P_{max}, CE, and R_D (Fig. 2). This supports the theory of convergence of leaf functioning (Reich *et al.* 1997). Increase of LMA is a common plant acclimation to high I, which results in increase of the ratio of leaf structural to assimilation components. LMA also influences the PAR transmission through and within leaves. This leaf trait is also closely and adversely correlated with leaf N content (Reich *et al.* 1997). It appears that leaf structural change such as change of LMA is the major component in plant acclimation to irradiance, and leaf N partitioning discussed above plays a role in the acclimation as well.

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