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Shade tolerance and suitability of tree species for planting in rubber plantations

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The rapid increase in rubber monoculture in Xishuangbanna has resulted in extensive damage to its local ecosystem. To decrease the negative effects, the concept of the ecological-economic rubber plantation (EERP) system was proposed. The EERP entails intercropping rubber plants with other economically significant plants, which would not only decrease the ecological impact of the rubber plantation, but also maintain and potentially increase its profitability compared with rubber monocultures. In order to select the appropriate species and intercropping pattern in the EERP system, we compared the photosynthetic parameters of five economically important trees (*Swietenia mahagoni*, *Coffea arabica*, *Mesua ferrea*, *Myristica yunnanensis* and *Paramichelia baillonii*) under four irradiance levels. The optimal irradiance intensity of *C. arabica* and *M. yunnanensis* was approximately 40%, and these species can be planted in the understory of an 8- to 15-year-old rubber forest. Adult *S. mahagoni*, *M. ferrea* and *P. baillonii* grow taller than the rubber trees, and their seedlings also show superior performance in 100% irradiance than in other irradiances. Thus, in an EERP, these valuable trees could be planted adjacent to rubber plantations but on sites that are economically and environmentally marginal for rubber production.

Keywords: bioenergetic, carboxylation, ecological-economic rubber plantation, leaf nitrogen allocation, photosynthesis

Introduction

Xishuangbanna, which is located in south-west China, is the most diverse region of the country, and has been included in the list of Indo-Burma biodiversity hotspots (Myers et al. 2000). Rubber (*Hevea brasiliensis*) is an important tree crop that is propagated in Xishuangbanna. The first rubber plantations were established in 1956 to meet the needs of national defence and economic development (Wu et al. 2001; Li et al. 2008). With the rapid increase in the price of rubber, an increasing number of natural forests were replaced by rubber plantations, and the rubber planting area in Xishuangbanna reached 270 000 ha by 2010, which was 800% higher than that of 10 years previously. Although rubber cultivation improves local economic and social situations, monoculture rubber plantations often cause various ecological problems, such as soil erosion, water deficiency, emission of volatile organic compounds (VOCs), and loss of biodiversity (Feng et al. 1982; Guo et al. 2002; Wang et al. 2007; Tan et al. 2011). In this context, the ecological-economic rubber plantation (EERP) system was recently established. The EERP concept proposes that rubber plants are intercropped with other native economic plants, which would not only decrease the ecological impact of rubber plantations, but also maintain and potentially increase profitability, compared with rubber monoculture.

One important step in the EERP system is the selection of appropriate species to intercrop with the rubber plants. In addition to the profitability of the target species, understory irradiance availability should also be considered. The interval between rubber planting and cutting is approximately 40 years, and understory irradiance gradually decreases with growth of the rubber tree. Irradiance is an important resource for plants, with survival, growth, and reproduction all depending on it. Photosynthesis is a process that is very sensitive to irradiance change (Niinemets et al. 1997; Valladares et al. 2000; Feng et al. 2007; Zheng et al. 2012). For example, leaf nitrogen (N) allocated to carboxylation (N_C) and bioenergetics (N_B) of the photosynthetic processes increase with higher levels of irradiance, whereas the fraction of leaf N allocated to light-harvesting components (P_L) and chlorophyll content decreases (Niinemets and Tenhunen 1997; McDowell 2002; Niinemets et al. 2003; Baltzer and Thomas 2007; Feng 2008; Zheng et al. 2012). These responses to irradiance increase the ability to capture light at low irradiance and increase the light-saturated photosynthetic rate (P_{max}). Although plants can grow in a broad irradiance range through plastic responses of physiological traits, each plant has an optimal irradiance range, where it can acquire its highest photosynthetic ability without photoinhibition or photodamage. Therefore, in the EERP system, economically significant species with different levels of shade tolerance should be intercropped with rubber trees using various patterns. For example, some species can grow in the understory of the rubber forest during an appropriate growth stage of rubber trees, whereas some sun-dependent species should be intercropped with rubber trees using a mosaic distribution pattern.

Swietenia mahagoni, *Coffea arabica*, *Mesua ferrea*, *Myristica yunnanensis* and *Paramichelia baillonii* are five economically significant crop trees in tropical areas. Previous studies have shown that shade tolerance differs among several species (Friend 1984; Ashton et al. 2006; Gonçalves et al. 2007). However, the species were not compared simultaneously. In the present study, the photosynthetic parameters of the five above-mentioned species were compared at four irradiance levels. The aims of the present study were to determine (1) the effects of irradiance on the photosynthetic system of the five species, and (2) the appropriate intercropping patterns for each species in an EERP system.

Materials and methods

Study site and species

This study was conducted at the Yunnan Institute of Tropical Crops located in Jinghong, Yunnan province, south-west China. The mean annual temperature of the area is 21.8 °C. The mean temperature in July, which is the hottest month, is 25.6 °C, and that in January, the coolest month, is 16 °C. The average annual precipitation is 1 235 mm, with a dry period lasting from November to April.

The five tropical species included in the present study are of high economic value. *Swietenia mahagoni*, *M. ferrea* and *P. baillonii* are tropical evergreen trees that grow to a height of 20–30 m. All three species are valuable timber species and are used in the construction of furniture, ships and musical instruments. *Coffea arabica* accounts for 75–80% of the world's coffee production. Commercial cultivars mostly grow to a height of approximately 5 m and are frequently trimmed to a height of 2 m to facilitate harvesting. *Myristica yunnanensis* is an evergreen tree that grows to a height of approximately 8 m, and its seeds and fruit are used in perfumes and oils.

Irradiance treatment

According to our investigation, the understory irradiance is approximately 40% (of full irradiance) for an 8-year-old rubber forest, 20% for a 15-year-old forest, and 10% for an up to 20-year-old forest (unpublished data).

In the present study, we created 40%, 20% and 10% irradiances by covering shadehouses with different layers of black nylon shade netting, including no netting to create 100% irradiance. The relative irradiance in each shadehouse was estimated by comparing the integrated photosynthetic photon flux density (PPFD) inside it during a clear day with that in the shadehouse with no netting. Quantum sensors and an Li-1400 datalogger (Li-Cor, Lincoln, NE, USA) were used to measure PPFD. To decrease potential differences among shadehouses due to environmental factors other than irradiance, the houses were constructed in a field and the lower 30 cm of each shadehouse remained open to facilitate airflow. To reduce possible irradiance heterogeneity within the houses, each shadehouse was divided into five sections and each section contained five seedlings of each species (see Appendix).

Seedlings

Seeds of the five species were sown in a seedbed in a greenhouse in July 2012. In September, when the seedlings were approximately 10 cm tall, seedlings of similar size were transplanted singly into 8 dm^3 plastic pots. A total of 500 pots were included in the study (5 species × 4 irradiances × 5 sections × 5 individuals). The pots were filled with equal proportions of sand and the top layer (0–20 cm depth) of local forest soil. Seedlings were watered with tap water every day.

Measurement

In December 2012, five seedlings (one seedling per section) per species per house were selected to determine the chlorophyll fluorescence of photosystem II (PSII) using a Dual PAM-100 fluorometer (Heinz Walz, Effeltrich, Germany) and photosynthetic response to intercellular CO_2 concentration (C_i) using a Li-6400 portable photosynthesis system (Li-Cor) on new fully expanded leaves. The maximum photochemical efficiency of PSII (F_v/F_m) was calculated as $F_v/F_m = (F_m - F_o)/F_m$. F_o represents the minimum fluorescence in the dark-adapted state, and F_m is the maximum fluorescence value upon illumination of a pulse (300 ms) of saturating light (10 000 μmol photons m^{-2} s^{-1}) in the dark-adapted state. $F_v = (F_m - F_o)$ is the variable fluorescence. Before determination of the photosynthetic response to C_i, we conducted a preliminary measurement to explore the saturating irradiance level and CO_2 concentration of each species in each house. Under a saturating level of irradiance, net photosynthetic rate (P_n) was measured at 400, 350, 300, 250, 200, 160, 130, 100, 80 and 50 μmol mol^{-1} CO_2 in the reference chamber. The relative humidity of the air in the leaf chamber was controlled at ~80% and the leaf temperature was maintained at 30 °C. The C_i and P_n of each leaf sample were recorded after 180 s at each CO_2 step. The photosynthetic rate was measured at 400 μmol mol^{-1} CO_2 and the saturating irradiance was P_{max}. Thereafter, the irradiance- and CO_2-saturated photosynthetic rate (P_{max}') were detected after 500 s under saturating irradiance and 1,800 μmol mol^{-1} CO_2. Before measurement, each leaf sample was illuminated with saturating irradiance provided by the light-emitting diode light source of the equipment for 5–30 min to achieve full photosynthetic induction. No photoinhibition occurred during the measurements.

Leaf discs (excluding the main vein) were taken from each sample leaf and oven-dried at 60 °C for 48 h. Leaf N content (N_M; g kg^{-1}) was determined using a Vario MAX CN Element Analyser (Elementar Analysensysteme GmbH, Hanau, Germany). Leaf chlorophyll (Chl) contents were measured following the method of Lichtenthaler and Wellburn (1983). The same leaf of each plant sample was used whenever possible for measurements of chlorophyll fluorescence, photosynthesis, Chl, and N_M, although in some cases similar leaves were used for some measurements.

Maximum carboxylation rate (V_{cmax}) was derived from P_n–C_i curves. Each P_n–C_i curve was fitted to a linear equation ($P_n = kC_i + i$) within 50–200 μmol mol^{-1} C_i, where k is the carboxylation efficiency (CE), and $-i/k$ is equal to the CO_2 compensation concentration (Γ^*) in the absence of mitochondrial respiration (Laisk et al. 2005), which was very low under irradiation. Maximum electron transport rate (J_{max}) was calculated using light- and CO_2-saturated photosynthetic rate. The contents of Rubisco and cytochrome (cyt) *f* were calculated using V_{cmax} and J_{max}, respectively. Nitrogen allocated to carboxylation (N_C) and to bioenergetics (N_B) was calculated using the levels of Rubisco and cyt *f*, respectively. The fraction of leaf N allocated to light-harvesting components (P_L) was calculated using chlorophyll content (C_C). Theories and calculations were based on Niinemets and Tenhunen (1997), Loustau et al. (1999), Warren and Adams (2004), Kitaoka and Koike (2004), Feng et al. (2007) and Feng and Fu (2008). The values of V_{cmax}, J_{max}, N_C, N_B and P_L were calculated using the following equations:

$$V_{cmax} = k[C_i + K_c(1 + O/K_o)]2/[\Gamma^* + K_c(1 + O/K_o)] \tag{1}$$

$$J_{max} = [4(P_{max}' + R_d)(C_i + 2\Gamma^*)]/(C_i - \Gamma^*) \tag{2}$$

$$N_C = V_{cmax}/(6.25 \times V_{cr}) \tag{3}$$

$$N_B = J_{max}/(8.06 \times J_{mc}) \tag{4}$$

$$P_L = C_C/(N_M \times C_B) \tag{5}$$

where K_c (Michaelis–Menten constant of Rubisco for carboxylation) and K_o (Michaelis–Menten constant of Rubisco for oxidation) are 275.1 μmol·mol^{-1} and 414.2 μmol mol^{-1} at 25 °C, respectively, and *O* (intercellular oxygen concentration) is 210 mmol mol^{-1} (Niinemets and Tenhunen 1997). V_{cr} (specific activity of Rubisco) and J_{mc} (the potential rate of photosynthetic electron transport per unit cyt *f*) are 20.78 μmol CO_2 g^{-1} Rubisco s^{-1} and 155.64 μmol electrons μmol^{-1} cyt *f* s^{-1} at 25 °C, respectively. C_B (the ratio of leaf chlorophyll to leaf N in light-harvesting components) is 2.15 mmol g^{-1}, and 6.25 (g Rubisco g^{-1} N in Rubisco) is the conversion coefficient between N content and protein content in Rubisco, and 8.06 (μmol cyt *f* g^{-1} N in bioenergetics) is the conversion coefficient between cyt *f* and N in bioenergetics (Niinemets et al. 1998).

Statistical analysis

A two-way analysis of variance (ANOVA) was used to test for the effects of species, irradiance and their inter-actions on each variable evaluated in this study. One-way ANOVAs (Duncan's multiple range test) were used to determine differences among irradiances in the same species for each variable. The significance of correlation between each pair of variables was tested using Pearson's correlation (two-tailed) analysis. Analyses were conducted using SPSS 17.0 (SPSS, Inc., Chicago, IL, USA).

Results

Two-way ANOVA showed that both species and irradiance imparted significant effects on all variables examined in the present study (Table 1). The interactions between species and irradiance were also significant, except for P_{max}, F_v/F_m and J_{max} (Table 1). With the decrease in irradiance, the P_{max} of *S. mahagoni*, *M. ferrea* and *P. baillonii* decreased, whereas *C. arabica* and *M. yunnanensis* showed the highest P_{max} at 40% irradiance (Figure 1a). The changing trends of V_{cmax} and J_{max} were similar to those of P_{max} (Figure 2a and b). No significant differences in F_v/F_m for *S. mahagoni*, *M. ferrea* and *P. baillonii* were observed among irradiances, whereas the F_v/F_m of *C. arabica* and *M. yunnanensis* under 100% irradiance was significantly lower than those under 40%, 20% and 10% irradiance (Figure 1b).

Table 1: Effects of species, irradiance and their interactions on each variable as indicated by two-way ANOVA

Variable	*F*-value		
	Species	Irradiance	Irradiance × Species
P_{max}	51.23***	11.04***	0.89
F_v/F_m	3.43*	4.96**	1.72
V_{cmax}	151.23***	11.04***	2.95**
J_{max}	24.70***	23.84***	1.74
N_C	74.48***	4.98**	1.98*
N_B	23.94***	28.75***	2.27*
P_L	7.52***	33.78***	2.67*
Chl	22.99***	38.57***	4.34***

* $P < 0.05$, * $P < 0.01$, * $P < 0.001$

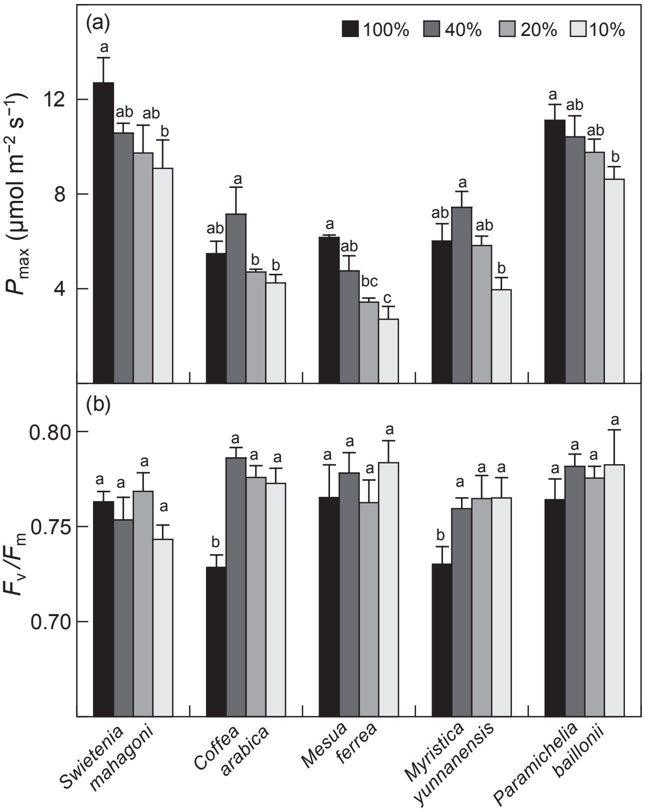

Figure 1: Light-saturated photosynthetic rate (P_{max}) of each species grown in four irradiances. Different letters above bars indicate significant differences among irradiances for each species

With the decrease in irradiance, N_C significantly decreased in *M. ferrea* and *P. baillonii*, but did not significantly change

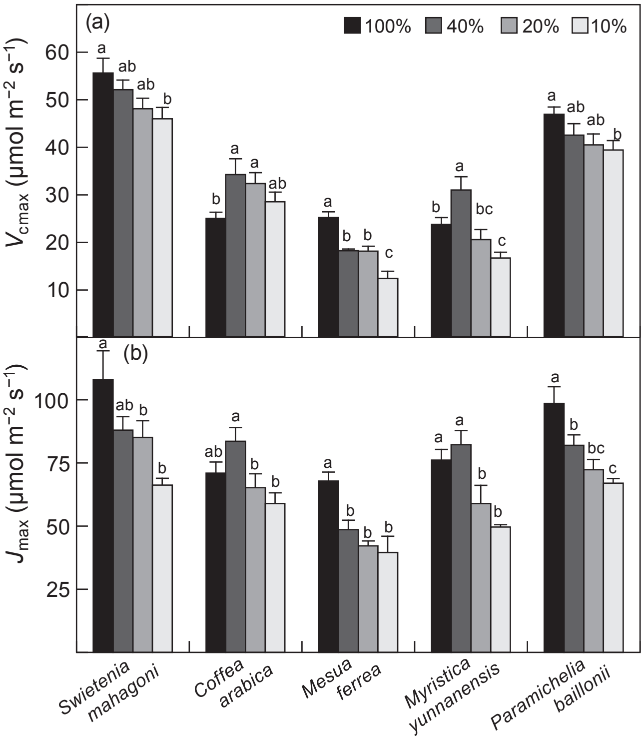

Figure 2: Maximum carboxylation rate (V_{cmax}) and maximum electron transport rate (J_{max}) of each species grown in four irradiances. Different letters above bars indicate significant differences among irradiances for each species

in *S. mahagoni* (Figure 3a). In *C. arabica*, N_C under 40% and 20% irradiance was significantly higher than that under 100% and 10% irradiance (Figure 3a). In *M. yunnanensis*, N_C under 20% irradiance did not significantly differ from that of the other three irradiance levels, whereas N_C in 10% irradiance was significantly lower than that under 100% and 40% irradiance (Figure 3a). With the decrease in irradiance, N_B significantly decreased in *S. mahagoni*, *M. ferrea* and *P. baillonii*, whereas in *C. arabica* and *M. yunnanensis* N_B slightly increased until 40% irradiance and then decreased (Figure 3b). For all species except *C. arabica*, the P_L under 100% irradiance was significantly lower than that under 20% and 10% irradiance levels (Figure 3c). For *C. arabica* and *M. ferrea*, the P_L in 40% irradiance was not significantly different from that under the other three irradiances, whereas for *M. yunnanensis* it was significantly higher than that under 100% irradiance, but lower than that under 20% and 10% irradiance (Figure 3c). However, the P_L of *S. mahagoni* under 40% irradiance was not significantly different from that under 20% and 10% irradiance, but was significantly higher than that under 100% irradiance (Figure 3c). The P_L of *P. baillonii* between 40% and 100% irradiances were not significantly different, and both were significantly lower than the P_L under 20% and 10% irradiance levels (Figure 3c). Except for *C. arabica* and *M. ferrea*, with the decrease in irradiance, the changing trend in chlorophyll content was the same with P_L (Figure 3c and d). In *M. ferrea*, no significant differences in chlorophyll content were observed among the various irradiance levels,

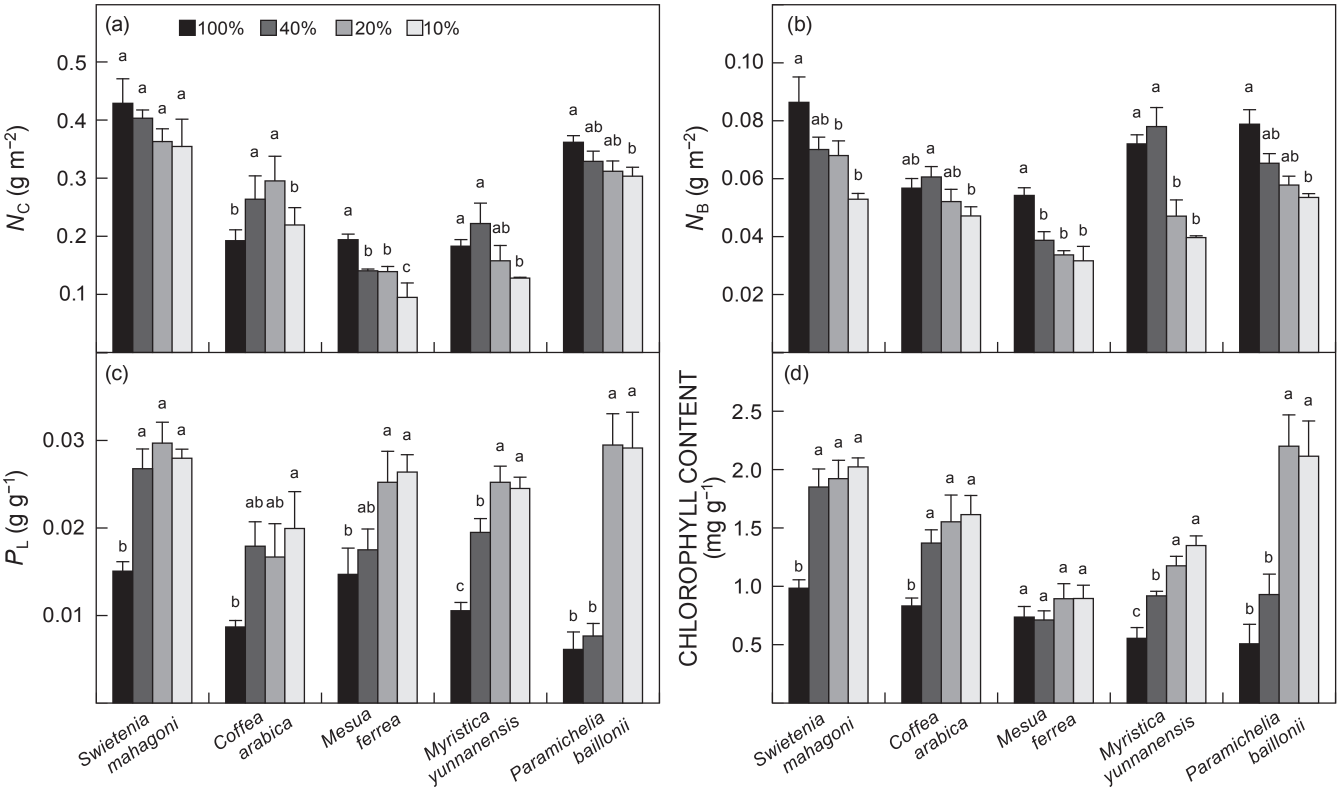

Figure 3: Nitrogen allocated to carboxylation (N_C) and to bioenergetics (N_B), leaf nitrogen allocated to light-harvesting components (P_L), and chlorophyll content of each species grown in four irradiances. Different letters above bars indicate significant differences among irradiances for each species

whereas in *C. arabica* the chlorophyll content under 100% irradiance was significantly lower than that observed in the other three irradiance levels (Figure 3d).

Discussion

For shade plants, high irradiance could lead to excessive production of energy during the photosynthesis of shade plants, causing photoinhibition and photodamage (Long et al. 1994; Huner et al. 1998). The F_v/F_m of *C. arabica* and *M. yunnanensis* with 100% irradiance was significantly lower than that observed under the 10%, 20% and 40% irradiance levels (Figure 2b), which indicated that 100% irradiance was stressful to both species. On the other hand, the highest P_{max} in *C. arabica* and *M. yunnanensis* was observed using 40% irradiance. It indicated that the optimal growing irradiance for *C. arabica* and M. yunnanensis was 40% irradiance. However, 100% irradiance was optimal for *S. mahagoni*, *M. ferrea* and *P. baillonii*, as indicated by their P_{max} and F_v/F_m at each irradiance level (Figure 1).

Nitrogen is one of the most important limiting resources for plant growth in nature, and most leaf N is allocated to photosynthesis (Takashima et al. 2004; Feng et al. 2007). Carboxylation, bioenergetics and light-harvesting systems are the three main components of photosynthesis. In the present study, V_{cmax} and J_{max} increased linearly with higher N_C and N_B, respectively (Figure 4a and b). P_{max} significantly increased with elevated N_B+N_C (Figure 4c), whereas no significant correlation was observed with P_L (Figure 4d). Previous studies have also shown that small changes in N allocation to each component significantly influence P_{max} and therefore plant performance (Onoda et al. 2004; Takashima et al. 2004; Feng et al. 2007; Feng and Fu 2008; Zheng et al. 2012). P_{max} showed no significant correlation with P_L (Figure 4d), which might be due to variation in V_{cmax} and J_{max} among species, leading to the same P_L although with different P_{max} values.

To facilitate harvesting in agricultural management, *C. arabica* and *M. yunnanensis* are frequently trimmed to a height of 2 m and 8 m, respectively. In an EERP system, *C. arabica* and *M. yunnanensis* can be planted in the understory of an 8- to 15-year-old rubber plantation (Figure 5a). Because the 8- to 15-year-old rubber trees in Xishuangbanna are approximately 10–15 m high, the understory irradiances are approximately 20–40%. According to the present study, *S. mahagoni*, *M. ferrea* and *P. baillonii* grow well in 100% irradiance. These are tropical evergreen trees of 20–30 m in height, and the interval from planting to harvesting is approximately 40 years. In the EERP system, these three species should be intercropped with rubber trees using a mosaic distribution pattern (Figure 5b). These three valuable trees could be planted

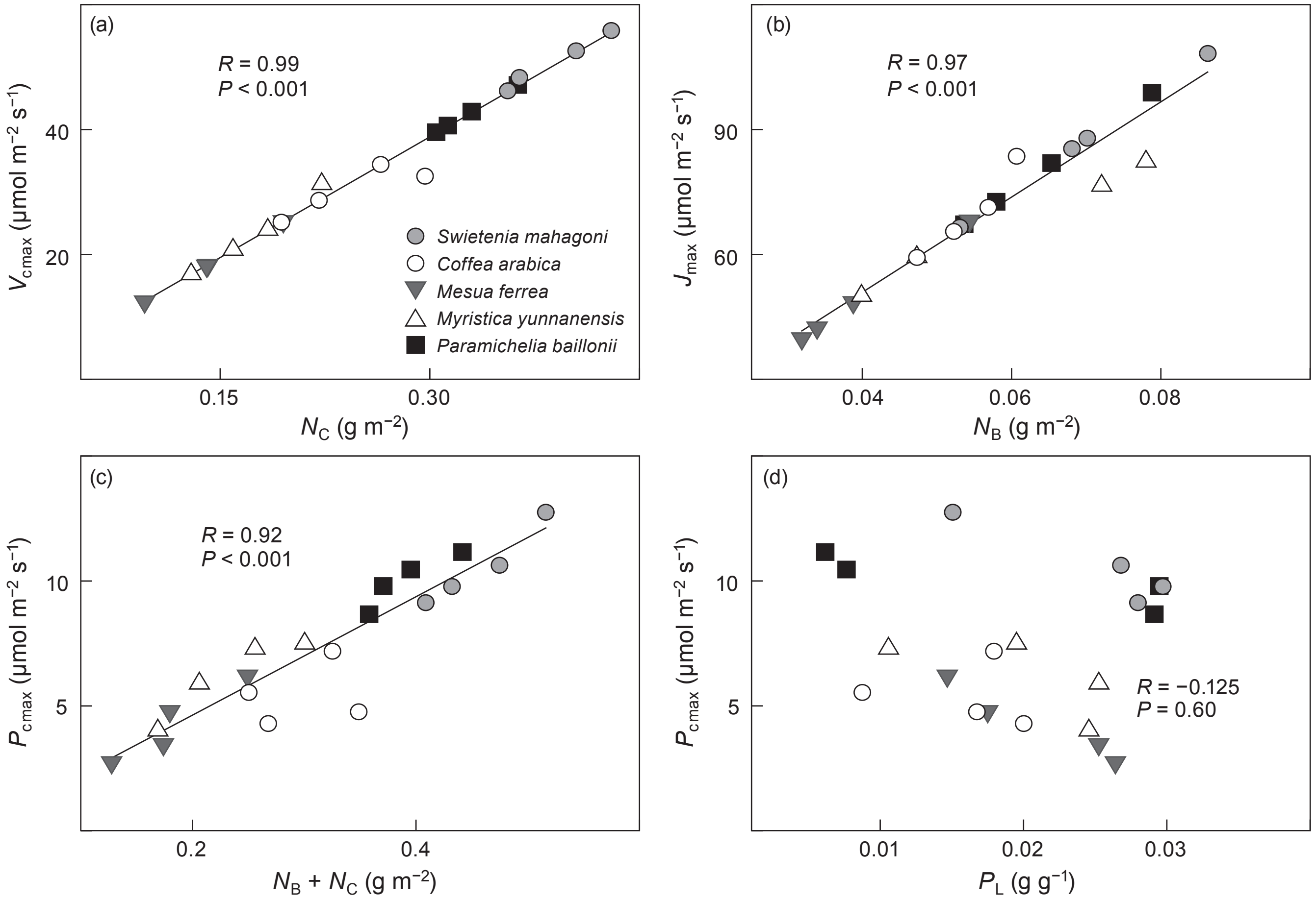

Figure 4: V_{cmax} as a function of N_C (a), J_{max} as a function of N_B (b), and P_{max} as a function of $N_B + N_C$ (c) and P_L (d) for each species

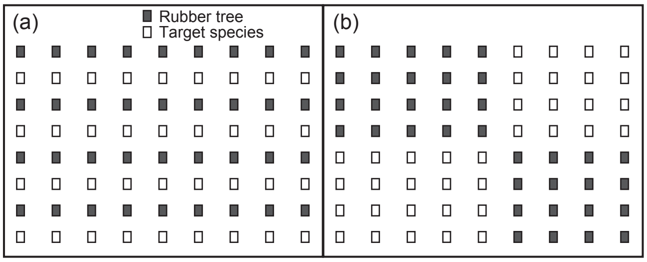

Figure 5: Two distribution patterns between rubber trees and economic species in an ecological-economic rubber plantation system. Target economic species grown in the rubber understory (a), and rubber tree and target species intercropped with a mosaic distribution pattern (b)

Table 2: Income of each crop tree species according to the market price (2014–2015) in China

Species	Use purpose	Unit price (CNY)	Income start (y)	Average income (CNY ha^{-1} y^{-1})
H. brasiliensis	Latex	10.00 kg^{-1}	7th	10 440
S. mahagoni	Timber	5 300.00 m^{-3}	20th	95 400
C. arabica	Beverage	3.50 kg^{-1}	3rd	42 000
M. ferrea	Timber	12 000.00 m^{-3}	70th	61 500
M. yunnanensis	Spice, medicine	4.00 kg^{-1}	7th	23 760
P. baillonii	Timber	1 950.00 m^{-3}	30th	21 450

adjacent to rubber plantations but on sites that are economically and environmentally marginal for rubber production.

Intercropping not only decreases soil erosion (Labrière et al. 2015) but also has the potential to increase profitability compared with monocropping (Rodrigo et al. 2005; CIRAD 2013). Based on market prices in China, the profitability of the five crop trees is also higher than rubber, and the investment income of most trees is very long (*S. mahagoni*, *M. ferrea* and *P. baillonii*) (Table 2), and the labour cost for *C. arabica* is higher than that for rubber. It will be more feasible if the government provided support or special policies for popularising the EERP system.

Conclusions

The irradiance level has a significant effect on the photosystem of each species studied, and N allocation plays an important role in acclimation to irradiance. In the EERP system, the planting pattern is site- and species-specific. *Coffea arabica* and *M. yunnanensis* could be planted in the understory of adult rubber forest, because the most suitable irradiance for the two species is 20–40%. In contrast, *S. mahagoni*, *M. ferrea* and *P. baillonii* grow well in full irradiance, therefore they should be planted in sites that are inconvenient or uneconomic for rubber plantation.

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Appendix: Distribution of each crop tree seedlings in the shadehouse. Five symbols represent five crop trees