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Light-response curve of photosynthesis and model fitting in leaves of *Mangifera indica* under different soil water conditions

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Abstract

A pot experiment was performed to study the light-response curve of photosynthesis (P_N-PAR curve) of *Mangifera indica* and the applicability of light-response models under different soil water conditions. The experimental data were fitted and analyzed using the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, the modified rectangular hyperbola model, and the kinetic model. The results showed that the optimal range of relative soil water content (RSWC) for the normal photosynthesis of *M. indica* was 45.1–77.3%. The modified rectangular hyperbola model could well fit the P_N-PAR curves and photosynthetic parameters under wide range of soil water conditions (RSWC 23.3–77.3%). The rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the kinetic model could only be used to fit the P_N-PAR curves of *M. indica* under mild and moderate drought stress (RSWC 45.1–77.3%).

Additional key words: field capacity; light-compensation point; light-response curve; model comparison; net photosynthetic rate.

Introduction

Photosynthesis is a biological process in which plants convert light energy into chemical energy that can be used in life processes and synthesize organic matter. In this process, the quantitative relationship between net photosynthetic rate (P_N) and photosynthetically active radiation (PAR) is the basis for revealing the response of the photosynthetic physiological process of plant to the environment (Govindjee and Krogmann 2004, Elfadl and Luukkanen 2006, Wang *et al*. 2017). The measurement and simulation of light-response curve of photosynthesis (P_N-PAR curve) is one of the important methods in studying the photosynthetic physiological ecology of plants. The main physiological parameters, such as maximum net photosynthetic rate (P_{Nmax}), apparent quantum yield (AQY), light-saturation point (LSP), light-compensation point (LCP), and dark respiration rate (R_D), can be obtained from the curve, which are helpful to determine the operation state of plant photosynthetic apparatus, photosynthetic capacity, and photosynthetic efficiency as well as an environmental changes influencing them (Sharp *et al*. 1984, Ye and Yu 2008a, Xia *et al*. 2014). Soil water content (SWC) is the major environmental factor affecting plant growth and metabolism, and drought stress often occurs and restricts plant growth and development, especially photosynthesis (Sofo *et al*. 2009, Ruzana Adibah and Ainuddin 2011, Wang *et al*. 2017). Therefore, it is important to study P_N-PAR curve under different soil water conditions to reveal quantitative relationship between photosynthetic characteristics and SWC.

Light-response model is essential for study of the P_N-PAR curve of plants. Many light-response models of photosynthesis have been constructed by experts (Bassman and Zwier 1991, Thornley 1998, Lewis *et al*. 1999), among which the rectangular hyperbola model, the nonrectangular hyperbola model, and the exponential model have been commonly used (Lang *et al*. 2013, Lobo *et al*. 2013, Xia *et al*. 2014, Wang *et al*. 2017, Duan *et al*. 2018). However, some researches have shown that there was deficiency in practical applications of the three models. The fitted values of photosynthetic parameters

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Abbreviations: AQY – apparent quantum yield; FC – field capacity; GWC – gravitational water content; LCP – light-compensation point; LSP – light-saturation point; P_N – net photosynthetic rate; P_{Nmax} – maximum net photosynthetic rate; P_N-PAR curve – light-response curve of photosynthesis; R^2 – determination coefficient; R_D – dark respiration rate; RSWC – relative soil water content; SWC – soil water content.

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were significantly different from the measured values (Ye 2007, Chen *et al*. 2011), and it was difficult to process experimental data under photoinhibition conditions, especially, the three models were only suitable for fitting the P_N-PAR curve and photosynthetic parameters under the normal soil water conditions (Lang *et al*. 2013, Xia *et al*. 2014, Wang *et al*. 2017). In recent years, Ye *et al*. (2007, 2008a,b) constructed a new light-response model – the modified rectangular hyperbola model, which was based on the rectangular hyperbola model. This new model may overcome the limitation of the traditional model and could accurately fit P_N-PAR curve and photosynthetic parameters under various environmental conditions (Ye 2007, Ye and Yu 2008b). Up to now, the modified rectangular hyperbola model has been applied to simulate the P_N-PAR curves of spring wheat, *Nicotiana tabacum* L., *Prunus sibirica* L., *Pinus tabulaeformis*, *Hippophae rhamnoides* L., *Ziziphus jujuba* var. *spinosus*, and *Populus euphratica* under different soil water conditions (Chen *et al*. 2011, Lang *et al*. 2013, Xia *et al*. 2014, Wang *et al*. 2017, Duan *et al*. 2018) and has achieved good results.

Mangifera indica, an evergreen tree belonging to the family of Anacardiaceae, is a typical perennial tropical fruit tree and enjoys the reputation of 'the king of tropical fruits' with remarkable economic benefits (Zang *et al*. 2009, Sarker *et al*. 2016). *M. indica* is mostly planted in mountain or hilly areas, and its growth and development is extremely vulnerable to drought stress during the dry season (Yao *et al*. 2006, Zang *et al*. 2009, Lu *et al*. 2012, Levin *et al*. 2018). At present, many studies have been done to investigate the photosynthetic characteristics (Yao *et al*. 2006, Elsheery and Cao 2008, Lu *et al*. 2012, dos Santos *et al*. 2013, 2014a, 2015), leaf physiological activity (Jia *et al*. 2000, Zaharah and Razi 2009, dos Santos *et al*. 2015), growth (Zaharah and Razi 2009), root distribution (dos Santos *et al*. 2014b), fruit yield (dos Santos *et al*. 2014a,b; 2015), and floral initiation (Bally *et al*. 2000, Chen *et al*. 2000, Lu and Chacko 2000) of *M. indica* under different soil water conditions or irrigation levels. In most studies, only a few water levels have been considered. It is necessary to obtain a sufficient amount of experimental data under multilevel SWC to accurately characterize the relationship between the photosynthesis and SWC. There was little information on the fitting and comparison of the P_N-PAR curve of *M. indica* under drought stress in previous studies. Therefore, we used two-year-old *M. indica* seedlings to measure P_N-PAR curves under different soil water conditions, fitted P_N-PAR curves and main photosynthetic parameters by the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, the modified rectangular hyperbola model, and the kinetic model. The aims of this study were to explore the relationship between photosynthesis and SWC, clarify the adaptability of these light-response models, and gain further understanding of the photosynthetic physiological characteristics of *M. indica* under different soil water conditions. The results could provide theoretical basis and practical guidance for soil water management of *M. indica* in actual production and cultivation.

Materials and methods

Experimental materials: Pot experiment was conducted in the research greenhouse of Faculty of Modern Agricultural Engineering, Kunming University of Science and Technology in Kunming, Yunnan, China (24°9'N, 102°79'E; 1,978.9 m a.s.l.) from May to August 2018. The greenhouse was oriented from north to south, and the light intensity was approximately 90% of the natural light. The length, span, and ridge height were 100, 21, and 3 m, respectively. The temperature was 20–35°C, the air humidity was 45–70%, and the CO_2 concentration was 365–395 μmol mol^{-1}. Changes of water surface evaporation in greenhouse during the experimental period were shown in Fig. 1. Two-year-old *Mangifera indica*. cv. Guifei seedlings were selected for the experiment. In May 2018, ten healthy seedlings with relatively uniform plant height and basal diameter were transplanted into white plastic buckets (44 cm in diameter at the top edge, 35 cm in diameter at the bottom, and 53 cm in depth). Six holes were uniformly punched at the bottom of bucket to provide better aeration. After 60 d for nursery, five seedlings of similar growth were selected for the measurement. The average plant height was 76.8 cm and the average basal diameter was 10.25 mm. The experimental soil was red loam, which was air dried and sieved (in a 2-mm sieve). The contents of organic matter, total N, total P, and total K in soil were 5.05, 0.87, 0.68, and 13.9 g kg^{-1}, respectively. Soil of 72 kg was added to each bucket; the soil was in average bulk density of 1.20 g cm^{-3} and average field capacity (FC) of 24.4%.

Acquisition of soil water gradient: Natural drought stress was applied on 10 July, 2018. Three days before the measurement of P_N-PAR curve, five experimental seedlings were provided by normal water supply (SWC reached FC of 85%), then the soil was naturally dried and no water was added. In order to obtain sufficient soil water gradients, the soil surface was covered with pine needles to slow down water evaporation. As soil water decreased gradually by evapotranspiration, the gravitational water content (GWC) and P_N-PAR curves were measured every three days, until the seedlings withered. GWC was measured by the convective oven-drying method, and the relative soil water content (RSWC) was the ratio of GWC to FC. All GWC and RSWC obtained during the experiment are shown in the text table:

Drought stress type	GWC [%]	RSWC [%]
Mild drought stress	18.88 ± 2.77	77.30 ± 4.69
	15.91 ± 1.40	65.14 ± 5.04
Moderate drought stress	13.38 ± 1.05	54.77 ± 5.10
	11.01 ± 0.92	45.06 ± 3.88
	8.99 ± 1.81	36.81 ± 4.50
Severe drought stress	6.89 ± 1.66	28.19 ± 3.14
	5.68 ± 0.93	23.25 ± 4.14

P_N-PAR curves were measured using the portable photosynthetic system (*LI-COR 6400*, *LI-COR Inc*., Lincoln, NE, USA) under different soil water conditions. After each SWC measurement, three healthy and mature leaves from the center of each seedling crown were selected and marked as fixed measured leaves. P_N-PAR curves were measured three times for each marked leaf, so that nine measurements were made for each seedling and 45 replications for each soil water gradient. The average value of 45 replications was taken for analysis. Measurements were made between 8:30–11:30 h on a sunny day under each soil water gradient. Before each measurement, the measured leaves were induced about 20–30 min at light intensity of 1,200 μmol(photon) m^{-2} s^{-1}. During the measurement, the flow rate of air in the measuring chamber was about 500 μmol s^{-2}, the atmospheric CO_2 concentration was maintained at 375 ± 5 μmol mol^{-1}, the temperature of the leaf chamber was 25 ± 1°C, and the relative humidity was 50 ± 5%. For every measurement, PAR was set at 2,000; 1,800; 1,500; 1,200; 1,000; 800, 600, 400, 200, 150, 100, 50, 20, and 0 μmol(photon) m^{-2} s^{-1} by artificial *Li-6400-02B* LED radiation source to measure P_N under different light intensities. For each PAR, the measurement time was controlled to 180 s and the photosynthetic parameters such as P_N were recorded automatically by the instrument.

P_N-PAR curves were drawn according to the measured data under different soil water conditions. P_{Nmax}, LCP, and R_D were estimated according to the trend of measured curve, and AQY was obtained by using the linear regression method of the P_N-PAR curve under weak light conditions [PAR ≤ 200 μmol(photon) m^{-2} s^{-1}]. The estimated photosynthetic parameters were considered the measured values and they were used to compare with the fitted values of following models.

Five light-response models

The rectangular hyperbola model (Lewis *et al.* 1999) was expressed as follows:

$$P_N = \frac{\alpha \times I \times P_{Nmax}}{\alpha \times I + P_{Nmax}} - R_D \quad (1)$$

where P_N is the net photosynthetic rate, α is the apparent quantum yield, P_{Nmax} is the maximum net photosynthetic rate, R_D is the dark respiration rate, and I is PAR.

If the measured data can be fitted well by the above model, LCP can be calculated by (Lang *et al.* 2013):

$$I_C = \frac{R_D \times P_{Nmax}}{\alpha \times (P_{Nmax} - R_D)} \quad (2)$$

where I_C is LCP.

The nonrectangular hyperbola model (Thornley *et al.* 1998) was expressed as follows:

$$P_N = \frac{\alpha \times I + P_{Nmax} - \sqrt{(\alpha \times I + P_{Nmax})^2 - 4 \times \theta \times \alpha \times I \times P_{Nmax}}}{2 \times \theta} - R_D \quad (3)$$

where θ (0 < θ ≤ 1) is the curvilinear angle of the nonrectangular hyperbola, and the other parameters are as described above.

If the measured data can be fitted well by the above model, LCP can be calculated by (Lang *et al.* 2013):

$$I_C = \frac{R_D \times P_{Nmax} - \theta \times R_D^{\,2}}{\alpha \times (P_{Nmax} - R_D)} \quad (4)$$

Exponential model: There are many different expressions for the exponential models. This research selected the exponential model proposed by Bassman and Zwier (1991):

$$P_N = P_{Nmax} \times (1 - e^{-(\alpha \times I)/P_{Nmax}}) - R_D \quad (5)$$

The parameters are as described above.

If the measured data can be fitted well by the above model, LCP can be calculated by (Wang *et al.* 2017):

$$I_C = \frac{-P_{Nmax}}{\alpha} \times \ln\left(\frac{P_{Nmax} - R_D}{P_{Nmax}}\right) \quad (6)$$

The modified rectangular hyperbola model (Ye 2007, Ye and Yu 2008a,b) was expressed as follows:

$$P_N = \alpha \times \frac{1 - \beta \times I}{1 + \gamma \times I} \times I - R_D \quad (7)$$

$$P_{Nmax} = \alpha \times \left(\frac{\sqrt{\beta + \gamma} - \sqrt{\beta}}{\gamma}\right)^2 - R_D \quad (8)$$

$$I_C = \frac{\alpha - \gamma \times R_D - \sqrt{(\gamma \times R_D - \alpha)^2 - 4 \times \alpha \times \beta \times R_D}}{2 \times \alpha \times \beta} \quad (9)$$

where β and γ are modified coefficients that are independent of I and the other parameters are as described above.

The kinetic model: The light-response process of plant photosynthesis conformed to the Michaelis-Menten equation of enzymatic kinetics. The kinetic model (Broadley *et al.* 2001) was expressed as follows:

$$P_N = \frac{P_{Nmax} \times (I - I_C)}{K_m + I - I_C} \quad (10)$$

where K_m is the value of I when P_N is half of P_{Nmax}, I_C is the value of I at which P_N reaches 0 (LCP), and the other parameters are as described above.

Statistical analysis: P_N-PAR curves and photosynthetic parameters were analyzed statistically and fitted nonlinearly by *Statistical Package for the Social Sciences 19.0* software for *Windows*. The experimental data

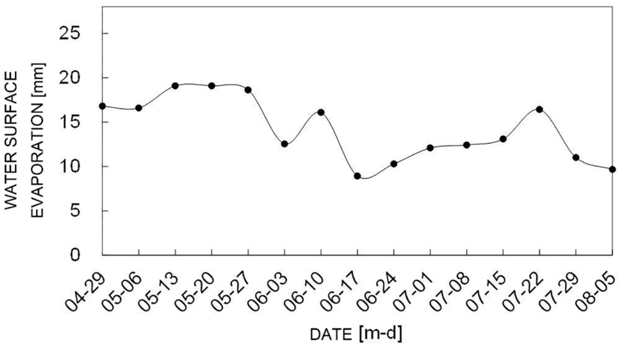

Fig. 1. Changes of water surface evaporation in the greenhouse during the experimental period from May to August 2018.

processing and drawing were performed by *Microsoft Excel* 2010. The initial values used in the models were: the rectangular hyperbola model: $\alpha = 0.05$, $P_{\mathrm{Nmax}} = 20$ μmol m^{-2} s^{-1}, $R_{\mathrm{D}} = 2$ μmol m^{-2} s^{-1}; the nonrectangular hyperbola model: $\alpha = 0.05$, $P_{\mathrm{Nmax}} = 20$ μmol m^{-2} s^{-1}, $\theta = 0.5$, $R_{\mathrm{D}} = 2$ μmol m^{-2} s^{-1}; the exponential model: $\alpha = 0.05$, $P_{\mathrm{Nmax}} = 20$ μmol m^{-2} s^{-1}, $R_{\mathrm{D}} = 2$ μmol m^{-2} s^{-1}; the modified rectangular hyperbola model: $\alpha = 0.01$, $\beta = 0.0001$, $\gamma = 0.001$, $R_{\mathrm{D}} = 2$ μmol m^{-2} s^{-1}; the kinetic model: $P_{\mathrm{Nmax}} = 20$ μmol m^{-2} s^{-1}, $I_{\mathrm{C}} = 40$ μmol m^{-2} s^{-1}, $K_{\mathrm{m}} = 300$ μmol m^{-2} s^{-1}.

Results

The P_{N}-PAR curves under different soil water conditions: The response of P_{N} to PAR was significantly diverse under different soil water conditions (Fig. 2). The P_{N}-PAR curves could be divided into three stages, among which the first and second stage showed a similar trend of the response regardless of RSWC. In the first stage, where PAR < 200 μmol(photon) m^{-2} s^{-1}, P_{N} increased linearly as PAR increased. With the further increase of PAR, the curves entered the second stage, P_{N} increased curvilinearly to saturation, and P_{Nmax} appeared. The P_{N}-PAR curves in the third stage were significantly different under different soil water conditions. Under mild and moderate drought stress, P_{N} reached saturation at PAR of 1,200 μmol(photon) m^{-2} s^{-1}, then P_{N} decreased slowly and maintained at a higher level without obvious photoinhibition. Under severe drought stress, P_{N} reached saturation at low PAR. When PAR > 800 μmol(photon) m^{-2} s^{-1}, P_{N} decreased significantly with the continuous increase of PAR and obvious photoinhibition was observed.

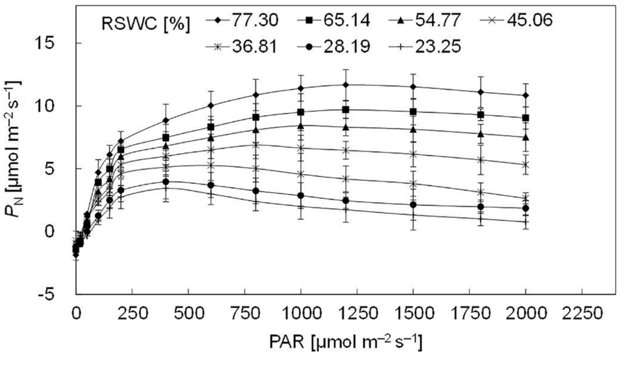

Fig. 2. The P_{N}-PAR curves of *Mangifera indica* under different soil water conditions. P_{N} – net photosynthetic rate; PAR – photosynthetically active radiation; RSWC – relative soil water content. Bars indicate ± SE of the mean, $n = 45$.

With the decrease of RSWC, P_{N} gradually decreased and the decreasing amplitude increased significantly under the same PAR. Compared to RSWC of 77.3%, P_{N} decreased by 16.6, 26.0, 41.7, 59.9, 74.8, and 82.3%, respectively, when RSWC was 65.1, 54.8, 45.1, 36.8, 28.2, and 23.3% at PAR of 1,000 μmol(photon) m^{-2} s^{-1}. Relatively higher P_{N}, LSP, P_{Nmax}, and less obvious photoinhibition were observed in the RSWC region of 45.1–77.3%. Thus, it could be considered that 45.1–77.3% was the suitable soil water range for the photosynthesis of *M. indica*.

Fitting of the P_{N}-PAR curves: The fitting effects of five light-response models on P_{N}-PAR curves were significantly different under different soil water conditions (Fig. 3). Except for the modified rectangular hyperbola model, there were significant discrepancies between the fitted and measured values of the other four models under high PAR, especially the discrepancies were more obvious under severe drought stress. In addition, P_{N}-PAR curves that were fitted by these four models were all asymptotic curves with no extreme value under high PAR. Particularly, under severe drought stress, they could not fit well the decline process of P_{N}. Among the all models, the rectangular hyperbola model and the nonrectangular hyperbola model had the worst fitting effects. The modified rectangular hyperbola model could well fit P_{N}-PAR curves under each soil water conditions and the fitting effect was the best as the fitted curves were consistent with the measured curves. Furthermore, only the modified rectangular hyperbola model could fit well the curves of P_{N} decreasing with the increase of PAR.

Fitting analysis of the photosynthetic parameters: The fitted results showed that under mild and moderate drought stress, all five light-response models had higher determination coefficients (R^2>0.94), and the fitting accuracy of the modified rectangular hyperbola model was the highest (R^2>0.99). Under severe drought stress, only R^2 of the modified rectangular hyperbola model was greater than 0.9, while R^2 of other four models ranged from 0.40–0.86 (Table 1). Therefore, the modified rectangular hyperbola model was the best way to fit P_{N}-PAR curves.

Under mild and moderate drought stress, the fitted values of R_{D} by five models showed no significant differences from the measured values. The fitted P_{Nmax} and LCP of the modified rectangular hyperbola model were close to the measured values. The fitted P_{Nmax} of other four models were higher than the measured values, while the fitted LCP were smaller than the measured values (Table 1). Under severe drought stress, only the modified rectangular hyperbola model had better the fitting effect on the photosynthetic parameters. For the other four models, the fitted values of photosynthetic parameters deviated

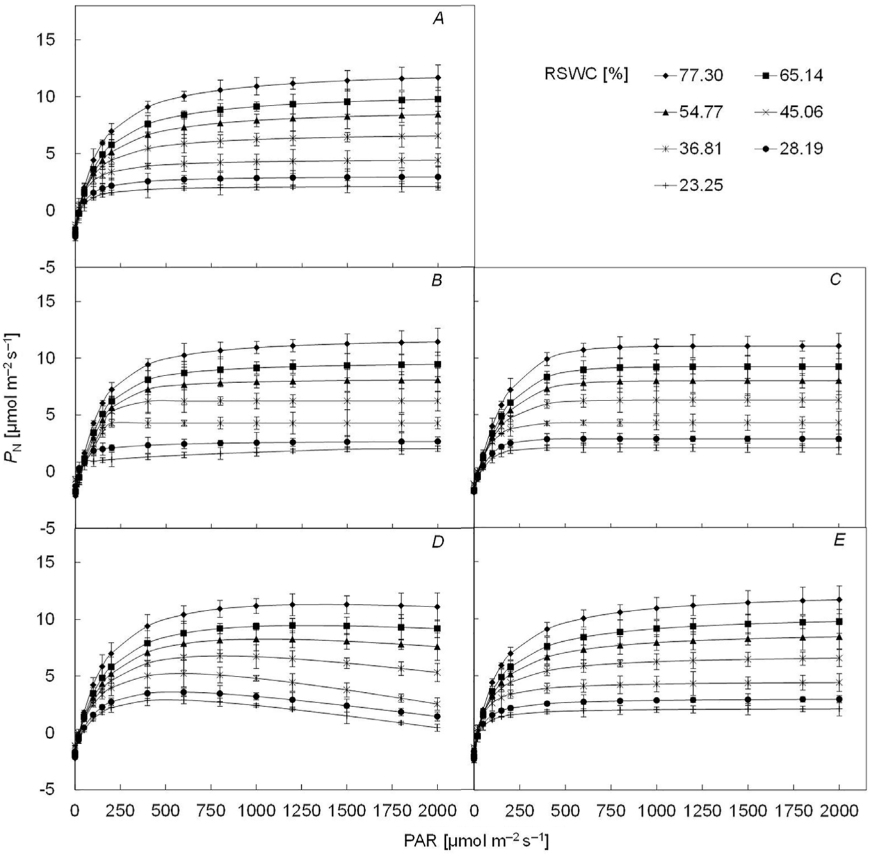

Fig. 3. Fitting of the P_N-PAR curves of *Mangifera indica* by the rectangular hyperbola model (*A*), the nonrectangular hyperbola model (*B*), the exponential model (*C*), the modified rectangular hyperbola model (*D*), and the kinetic model (*E*) under different soil water conditions. P_N − net photosynthetic rate; PAR − photosynthetically active radiation; RSWC − relative soil water content. Bars indicate ± SE of the mean, $n = 45$.

more from the measured values. By the comparison and analysis, the fitting effects of five light-response models on the photosynthetic parameters were in the descending order: the modified rectangular hyperbola model, the exponential model, the kinetic model, the nonrectangular hyperbola model, and the rectangular hyperbola model.

As shown in Table 1, AQY and P_{Nmax} decreased continually with the decrease of RSWC. Under mild and moderate drought stress, R_D and LCP decreased gradually with the decrease of RSWC. However, R_D and LCP increased significantly under severe drought stress.

Discussion

Photosynthesis cannot proceed normally when soil water is seriously inadequate (Beis and Patakas 2012, Xia *et al.* 2014). Drought stress can lead to the decrease of P_N depending on the stress level; mild water deficit has no significant effect or can even increase P_N, while severe water deficit can decrease P_N significantly (Zhang *et al.* 2007, Xia *et al.* 2011, Lang *et al.* 2013). Therefore, soil water is an important environmental factor that can directly regulate photosynthesis, water physiology, and metabolism of plants (Hu *et al.* 2004, Sofo *et al.* 2009, Wang *et al.* 2017). In this research, we found that P_N decreased significantly with the decrease of RSWC under the same PAR and the degree of photoinhibition was significantly related to RSWC in *M. indica*. High P_N was maintained and no photoinhibition occurred under mild and moderate drought stress. In contrast, obvious photoinhibition occurred and P_N decreased significantly under severe drought stress, which was n agreement with the results showing that photoinhibition can reduce photosynthetic productivity under low RSWC and high PAR (Lang *et al.* 2013). Previous studies have shown that water deficit is a common limiting factor in the photosynthesis and water deficit remarkably reduced P_N, possibly due to the decrease of stomatal conductance, the obstruction of CO_2 diffusion into leaves, or the decline of photosynthetic activity of mesophyll cells induced by drought stress (Galmés *et al.* 2007, Pascual *et al.* 2010, Chastain *et al.* 2014).

The fitting of light-response model is an important method to elucidate the response mechanism of photosynthesis and evaluate the photosynthetic efficiency (Wang *et al.* 2017). In our research, the fitting effects of five light-response models on the P_N-PAR curves of *M. indica* were compared under different soil water conditions. The fitting effects of the rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the kinetic model on P_N-PAR curves were better ($R^2 > 0.9$) only under mild and moderate drought stress. These four models could not fit the decline process of P_N-PAR curves when severe drought stress and photoinhibition occurred, which indicated that the application and fitting accuracy of above four models were largely limited under severe drought stress, because each model is an asymptotically saturating curve without a clear maximum within the range of the data (Lang *et al.* 2013). We also found that the fitting effect of the rectangular hyperbola model was the worst when photoinhibition occurred, which was

Table 1. The measured apparent quantum yield (AQY), maximum net photosynthetic rate (P_{Nmax}), dark respiration rate (R_{D}), and light-compensation point (LCP), and their fitted values using five light-response models for *Mangifera indica* under different relative soil water contents (RSWC). Each value is the mean of 45 replications and the determination coefficient (R^2) is listed for each model.

Light response model	Photosynthetic parameter	RSWC [%]						
		77.30	65.14	54.77	45.06	36.81	28.19	23.25
Measured value	AQY	0.047	0.042	0.038	0.030	0.027	0.024	0.020
	P_{Nmax} [μmol m^{-2} s^{-1}]	11.675	9.702	8.441	6.891	5.274	3.970	3.451
	R_{D} [μmol m^{-2} s^{-1}]	1.857	1.402	1.225	0.954	0.714	1.177	1.200
	LCP [μmol m^{-2} s^{-1}]	39.364	33.721	32.588	30.706	26.752	49.894	59.721
Rectangular hyperbola model	AQY	0.126	0.105	0.097	0.098	0.116	0.101	0.096
	P_{Nmax} [μmol m^{-2} s^{-1}]	14.916	12.559	10.804	8.306	5.803	4.714	3.691
	R_{D} [μmol m^{-2} s^{-1}]	2.418	2.070	1.813	1.422	1.257	1.650	1.529
	LCP [μmol m^{-2} s^{-1}]	22.903	23.605	22.460	17.418	13.748	25.251	26.949
	R^2	0.991	0.983	0.977	0.941	0.773	0.740	0.598
Nonrectangular hyperbola model	AQY	0.088	0.063	0.048	0.031	0.028	0.025	0.022
	P_{Nmax} [μmol m^{-2} s^{-1}]	14.086	11.500	9.606	6.964	4.953	3.059	2.341
	R_{D} [μmol m^{-2} s^{-1}]	2.143	1.770	0.861	0.732	0.683	1.275	1.344
	LCP [μmol m^{-2} s^{-1}]	26.288	29.414	18.183	23.627	19.408	36.036	45.091
	R^2	0.993	0.991	0.991	0.976	0.863	0.720	0.409
Exponential model	AQY	0.078	0.068	0.062	0.058	0.062	0.056	0.048
	P_{Nmax} [μmol m^{-2} s^{-1}]	12.949	10.971	9.504	7.444	5.426	4.480	3.549
	R_{D} [μmol m^{-2} s^{-1}]	1.887	1.735	1.511	1.162	1.144	1.625	1.493
	LCP [μmol m^{-2} s^{-1}]	26.147	27.774	26.542	21.783	20.722	36.044	40.363
	R^2	0.989	0.987	0.990	0.973	0.846	0.829	0.693
Modified rectangular hyperbola model	AQY	0.107	0.087	0.074	0.062	0.060	0.058	0.048
	P_{Nmax} [μmol m^{-2} s^{-1}]	11.553	9.602	8.200	6.506	5.908	4.016	3.891
	R_{D} [μmol m^{-2} s^{-1}]	2.232	1.920	1.601	1.152	0.904	1.125	1.311
	LCP [μmol m^{-2} s^{-1}]	31.909	25.497	24.918	20.622	24.813	51.246	61.580
	R^2	0.994	0.990	0.992	0.992	0.982	0.947	0.933
Kinetic model	AQY	0.045	0.038	0.034	0.028	0.021	0.017	0.014
	P_{Nmax} [μmol m^{-2} s^{-1}]	12.497	10.481	8.989	6.890	4.551	3.059	2.170
	R_{D} [μmol m^{-2} s^{-1}]	2.419	2.078	1.815	1.416	1.251	1.655	1.521
	LCP [μmol m^{-2} s^{-1}]	22.922	23.807	22.390	17.386	13.798	25.223	27.019
	R^2	0.991	0.983	0.977	0.941	0.773	0.740	0.598

perhaps because the curved degree of P_{N}-PAR curve was not considered in this model (Wang *et al.* 2017). The fitted P_{Nmax} values were significantly higher than the measured values, while the fitted LCP values were lower than the measured values, thus, the photosynthetic parameters fitted by these four models deviated greatly from the measured values. The modified rectangular hyperbola model could fit well the P_{N}-PAR curves and photosynthetic parameters of *M. indica* under mild and moderate drought stress. Meanwhile, this model can also well fit the photoinhibition response trend (R^2>0.9) even under severe drought stress, and the fitted values of photosynthetic parameters deviated less from the measured values. This indicated that the model was insensitive to drought stress and suitable for fitting P_{N}-PAR curves under a wide range of soil water conditions. Thus, the fitting effect of this model was better than that of the other models and it could analyze the light-response data more accurately under photoinhibition conditions. This was related to the addition of two parameters (β and γ) into this model, which made the model highly advantageous in fitting the photoinhibition and light-saturation stages under severe drought stress (Ye 2007, Ye and Yu 2008b).

The main photosynthetic parameters can be quickly estimated by light-response model. The P_{Nmax} represents the maximum photosynthetic capacity of leaves and also reflects the maximum assimilation capacity under certain environmental conditions (Duan *et al.* 2018). The P_{Nmax} of *M. indica* significantly decreased with the decrease of RSWC. The results showed that the decrease of RSWC can lead to the decrease of the ability to utilize strong light, the narrowing of photosynthetically active range, and the decrease of photosynthesis and organic matter production capacity of *M. indica*. AQY is an important indicator of light-utilization efficiency. The common method of calculating AQY is to use the slope of P_N-PAR curves when PAR ≤ 200 µmol(photon) m^{-2} s^{-1}. Results based on this method have shown that the range of AQY is from 0.03 to 0.05 in common plants under optimal conditions (Wang *et al*. 2017). In this experiment, we found that the AQY of *M. indica* decreased with the decrease of RSWC and it was in the range of 0.020–0.047 under different soil water conditions. The AQY was of 0.030–0.047 under mild and moderate drought stress and *M. indica* showed the maximum AQY of 0.047 under RSWC of 77.3%. This result indicated that the light-utilization efficiency of *M. indica* was at the common level for most plants under low light and optimal soil water conditions. Ye and Yu (2008a) thought that LCP is a more reasonable indicator to evaluate the light-utilization efficiency under low light intensity, because LCP is invariant under specific environment. R_D is related to physiological activity of leaves. In our research, we found that R_D and LCP decreased gradually with the decrease of RSWC under mild and moderate drought stress. The results illustrated that the decrease of RSWC could reduce the physiological activity of leaves, but *M. indica* could resist drought stress and adapt to drought environment by increasing the ability to utilize and transform weak light and accumulating organic matter by reducing consumption of photosynthates in a certain range. R_D and LCP increased significantly under severe drought stress, indicating that the ability of *M. indica* to utilize weak light decreased under these conditions. Under severe drought stress, the photosynthetic apparatus of *M. indica* may be damaged to a certain extent and the ability to produce organic matter decreased, while the respiration consumption increased, which was not conducive to accumulation of assimilated product and ultimately led to the imbalance of nutritive material supply and demand. The LSP was not listed and compared in Table 1, because the five light-response models all function without extreme values and the LSP value cannot be accurately calculated (Lang *et al*. 2013, Duan *et al*. 2018). Relevant research has shown that it was a gradual change process for P_N from unsaturated to saturated state, so LSP should be a range, not a definite point (Duan *et al*. 2018).

Photosynthesis is the basis of plant growth and development and the decisive factor of plant productivity and crop yield. It is also an important reference index for plant breeding, cultivation, and the response to environmental stress (Hu *et al*. 2004, Xu *et al*. 2012, Wu *et al*. 2018). Light is a crucial environmental factor in the photosynthesis (Xia *et al*. 2011). However, when the light energy absorbed by plants exceeds their needs, the excessive excitation energy can cause photoinhibition and reduce photosynthetic efficiency. High light, together with drought stress, breaks the balance between CO_2 fixation and light absorption within chloroplasts during photosynthesis, resulting in further accumulation of excessive light energy and intensifying photoinhibition (Lang *et al*. 2013). Moreover, serious photoinhibition can even destroy the photosynthetic apparatus (D'Ambrosio *et al.* 2006). In order to avoid photoinhibition, shading or irrigation are often used to ensure the normal photosynthesis and improve photosynthetic efficiency when PAR is too high in agricultural production.

In this study, *M. indica* grew poorly and the leaves withered and fell off after suffering from severe drought stress. Thus, RSWC must be maintained at more than 45% in cultivated soil to ensure the normal growth and photosynthesis of *M. indica*. In addition, transplanting of *M. indica* seedling should avoid serious arid regions or seasons as far as possible, which can reduce the influence of photoinhibition and the damage of photosynthetic apparatus in leaves to improve the survival rate to a certain extent.

Conclusion: The photosynthesis process and efficiency of *M. indica* were significantly inhibited and the degree of photoinhibition was intensified under severe drought stress (RSWC from 23.3 to 36.8%). AQY and P_{Nmax} could still maintain higher under mild and moderate drought stress (RSWC from 45.1 to 77.3%), while decreased significantly under severe drought stress. The light-response model had different adaptability to the P_N-PAR curves of *M. indica* under different soil water conditions. The rectangular hyperbola model, the nonrectangular hyperbola model, the exponential model, and the kinetic model were only suitable for fitting P_N-PAR curves under mild and moderate drought stress, but the modified rectangular hyperbola model could perfectly fit P_N-PAR curves under a wide range of soil water conditions (RSWC from 23.3% to 77.3%) and the estimation of photosynthetic parameters was more accurate. Especially under severe drought stress, the modified rectangular hyperbola model had better applicability. It was optimal for the normal growth and photosynthesis of *M. indica* when RSWC was from 45.1 to 77.3%, indicating that *M. indica* had strong drought resistance and the wide adaptation range to soil water content.

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