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Vegetative growth and photosynthesis in coffee plants under different watering and fertilization managements in Yunnan, SW China

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Abstract

In a field experiment *Coffea arabica* L. was subjected to various moisture and fertilizer regimes in Simao, Yunan, SW China. The experimental treatments consisted of eight factorial combinations of two fertilization levels (high and low) and four watering treatments applied in the dry season: application of dry rice straw mulch, drip irrigation, mulching plus drip irrigation on the soil surface, and control (no mulching or irrigation). The growth of the coffee plants was monitored throughout the course of a full year. Two clear growth peaks were detected (one at the beginning and one in the middle of the wet season) in plants subjected to all treatments, and the growth rhythm of coffee plants was not regulated by extrinsic abiotic factors. High fertilization resulted in a significantly higher relative growth rates for both height and length of the branches during the growth peaks than the low fertilization treatment. In the dry season, increasing the soil moisture contents by irrigation and/or mulching enhanced the plants' gas exchange, but the soil water status had no significant effects on the internal fluorescence parameters of photosystem 2. More fertilized plants had a greater ability to acclimate to high-irradiance environments than the lightly fertilized plants, showing significant lower diurnal photoinhibition, associated with higher energy utilization through photochemistry and energy dissipation through the xanthophyll cycle. Hence the wet season is the optimum period for photosynthetic carbon fixation and vegetative growth of coffee plants. Higher than routinely applied levels of fertilization are required to optimize the coffee plants' photosynthetic acclimation and growth in the studied environment. Both soil moisture conserving practices tested, mulching and drip irrigation, had significant effects on the growth and photosynthesis of the coffee plants, but the former was more practical than the latter.

Additional key words: chlorophyll fluorescence kinetics; *Coffea arabica*; drip irrigation; gas exchange parameters; mulching; photochemical efficiency; relative growth rate; stomatal conductance; transpiration rate; water use efficiency.

Introduction

Coffee was introduced to China more than 100 years ago. *Coffea arabica* L. was the dominant planted coffee species and was widely cultivated in the tropical and subtropical regions in southwest China (Long and Wang 1997). Coffee was originally classified as obligatory shade species. Strong irradiation at midday usually induces severe photoinhibition and photo-oxidative damage of photosynthetic apparatus of coffee leaves (Nunes *et al.* 1993, Da Matta and Maestri 1997). A number of environmental stresses, including drought and malnutrition, may increase coffee plants' sensitivity to photoinhibition and photodamage, induce cellular damage, and thus decrease their productivity (Nunes *et al.* 1993, Da Matta *et al*. 1997, 2002, Da Matta 2004, Cai *et al.* 2005).

Coffee plants require high levels of nutrients and are sensitive to drought (Barros *et al.* 1995, Da Matta *et al*. 2003, Cai *et al*. 2004). The growth and yield of coffee are confined to both dry and nutrient-poor soils because most lands for coffee plantation are located in mountainous areas in China. Soil water deficit in the dry season is amongst the main environmental factors that largely limit the productivity of coffee (Long and Wang 1997), although the ability of different coffee plant lines to survive water stress and maintain satisfactory levels of productivity in areas subjected to water deficit varies. Resistant lines display a suit of morphological and physiological adaptations, including leaf area reductions,

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adjustment to their stomatal closure response, osmotic status, and non-radiative energy dissipation mechanisms (Da Matta *et al.* 2002, 2003, Cai *et al.* 2005). In addition, agricultural practices can help reduce potential water deficits and, thus, boost crop productivity. Supplementary drip irrigation and rice straw mulching on the soil surface have been employed in many parts of China for centuries to increase soil moisture in the field (Sun *et al.* 2001). Mulching is one of the simplest and most beneficial crop cultivation practices, which, in addition to improving the water status of many soils, help control weed growth (Erenstien 2002), retain soil moisture (Enrique *et al.* 1999, Rahmana *et al.* 2005), and reduce losses of nutrients applied in fertilizers (Bhagat and Verma 1991).

The agronomic traits of coffee plants are well characterized (Barros *et al*. 1995, Da Matta 2004) and the interactive effects of nutrition and water availability on their growth and leaf photosynthesis have been well documented (*e.g*. Da Matta *et al.* 2002). However, physiological and biochemical characteristics of coffee plants under water- and nutrient-limited conditions have been less thoroughly studied, and information relating to mulch management and fertilization requirements in field-grown coffee plants is scarce. The objectives of this study were: (*1*) to study the vegetative growth and photosynthesis of coffee plants in the field under both optimal water and nutrient conditions and suboptimal conditions, *i.e*. under water and/or nutrient stress, and (*2*) to compare the effects of various water managements on the growth and photosynthesis of coffee plants.

Materials and methods

Soil and climate: The experiment was conducted during two consecutive years of 2002–2003 in the field in the Coffee Plant Centre in Simao (22°67'N, 100°88'E, 1 050 m a.s.l.), Yunnan, China, where 4 500 coffee plants per ha were cultivated. The soil (0–20 cm) at this site is characterized as an acidic lateritic red soil with pH 5.4 and 2.0 g kg^{-1} exchangeable calcium. Organic matter and total N and P contents of the soil were 2.870, 0.169, and 0.116 g kg^{-1}, respectively, while the available N and P contents were 145.1 and 10.1 mg kg^{-1}, respectively. The texture of the soil surface layer was loam, but there was a thin sub-surface layer of sand that enhanced percolation and drainage of the soil. Monthly rainfall and average air temperature in 2002, recorded at the meteorological station nearby, are presented in Fig. 1. There was a clear alternation of dry (November to April) and wet (May to October) seasons in the local area. The monthly rainfall at the research field ranged from less than 65 mm in February in the dry season to over 350 mm in July and August during the wet season. The mean air temperature is 19.8 °C, and the lowest temperature (13.6 °C) occurs in December.

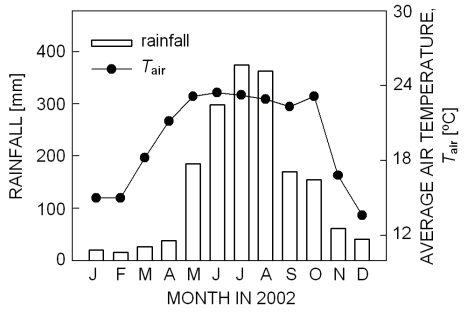

Fig. 1. Average monthly air temperatures (T_{air}) and rainfall in 2002 at the studied site.

Experimental design and treatments: Five-year-old coffee plants were separated to eight sub-groups that were each subjected to one of eight factorial combinations of four watering treatments and two fertilizer levels. The four watering treatments were application of: 3.0 Mg ha^{-1} sun-dried rice straw mulch; drip irrigation; mulch plus drip irrigation on the soil surface; and control (no irrigation or mulching). In the drip irrigation treatments, which were applied from December 2001 to April 2002 in the dry season, the soil was irrigated every week from 08:00 to 10:00 in the morning using plastic tubes with three dripping pores per meter at the rate of 3 800 cm^3 $pore^{-1}$ h^{-1}. Two levels of fertilizations were: normal fertilization that is actually used in the field by the local farmers (300 g oilseed rape, 60 g urea, 100 g compound fertilizer, and 1 000 g manure for one plant per year); high fertilization (another 60 g compound fertilizer with N:P:K ratio at 1:1:1 was added per plant besides the normal fertilization). Twelve to fifteen coffee individuals were selected for each treatment. The fertilization treatments were started in December 2001 and plants were fertilized once every three months.

Soil water status and leaf N content: Samples from the upper 20 cm soil layer representing each treatment were collected during the wet and dry seasons to determine soil moisture content gravimetrically. The soil water holding capacity (23.1 %) was determined following Piper (1944) and the relative soil water content (RSWC %) was calculated. Total N content of leaves in the wet season was measured by the semi-micro-Kjeldahl digestion method.

Growth: In January 2002, eight coffee plants per treatment were labelled for the growth measurement and four primary plagiotropic branches per plant were tagged in the upper third of the canopy for periodical length measurements. The height of the plants and the length of branch were determined every month from February 2002 to January 2003. The numbers of branch pairs of coffee and new sprouting branches were also counted. The relative growth rate (RGR) was calculated as: $RGR = (H_{t+1} - H_t)\ t^{-1}$, where t is the time in months.

Photosynthesis and leaf reflectance measurements: Gas exchange was determined in the morning between 10:00 and 11:00 h, which was presumed to be the diurnal period when photosynthetic rates would be maximal. Gas exchange parameters (net photosynthetic rate, P_N; stomatal conductance, g_s; transpiration rate, E; and water use efficiency, WUE) were measured using a portable infrared gas analyzer in open system mode (*LI-6400, Li-Cor*) under ambient CO_2 concentration and saturating irradiance (1 100 μmol m^{-2} s^{-1}, provided by a built-in red LED radiation source). Chlorophyll *a* fluorescence was measured using a portable pulse-modulated fluorescence system (*FMS2.02*, *Hansatech*, UK). Leaves, dark-adapted for 30 min, were irradiated with a weak modulated measuring beam to obtain the initial fluorescence (F_0). A saturating "white light" pulse of 6 000 μmol m^{-2} s^{-1} was applied for 0.7 s to obtain the maximum fluorescence emission (F_m). F_s was determined when the fluorescence became stable and F_m' was obtained by applying a strong pulse. The initial and actual photochemical efficiencies of PS2 were then calculated as $F_v/F_m = (F_m - F_0)/F_m$ and $\Delta F_v'/F_m' = (F_m' - F_s)/F_m'$. $\Delta F_v'/F_m'$ was determined between 10:00 and 11:00 h in the morning. F_v/F_m was measured at predawn (06:30) and midday (13:00). The diurnal change was estimated as: % diurnal photoinhibition = $100 - [(F_v/F_{m13:00})/(F_v/F_{m06:30})]\times 100$.

A *UniSpec* Spectral Analysis System (*PP Systems,* Haverhill, MA, USA) was used to measure spectral reflectance at wavelengths from 306 to 1 138 nm. A spectral reflectance standard was regularly referenced and scans were corrected for the instrument's dark current. Each scan represented the mean of four passes and the instrument's integration time was set at 125 ms. The photochemical reflectance index, which was calculated as $PRI = (R_{531} - R_{570})/(R_{531} + R_{570})$ (Gamon and Surgus 1999), was correlated with the epoxidation state of xanthophyll cycle pigments and photosynthetic radiation-use efficiency (net photosynthesis/incident PAR) (Gamon *et al*. 1992). The method used to estimate xanthophyll pigment activity was to sample PRI under both predawn and midday irradiances on the same leaf to derive a ΔPRI (expressed as the predawn PRI minus the midday PRI values), and thus the resulting values provided indications of the conversion of xanthophyll cycle pigments used in photo-protection under ambient irradiance (Gamon and Surgus 1999). All measurements were made on fully expanded and healthy upper canopy leaves from plagiotropic branches in March (dry season) and June (wet season) in 2002. The number of plants per light treatment for physiological measurements ranged from four to six; one leaf per plant was measured.

Statistical analyses: The statistical differences of between-treatment and between-season differences in the measured growth and photosynthetic parameters were analyzed using Student's *t*-test with *SPSS 11.0* (Chicago, IL, USA). Main and interactive effects of watering and fertilization treatments on physiological traits in the dry season were tested by two-way ANOVA. Differences were considered significant at a probability level of $p<0.05$.

Results

Soil moisture and leaf N content: The relative water content (RSWC) of the surface layer (0–20 cm) of the soil in the wet season was over 95 % of the field water-holding capacity and was similar among different treatments. Soil moisture was not affected by fertilization, but RSWC clearly increased following applications of rice straw mulch, drip irrigation, and mulch plus drip irrigation in the dry season ($p<0.05$). The leaf N contents of the coffee plants ranged from 2.34 to 3.12 % (Table 1). Compared to the low fertilization treatment, high fertilization significantly increased leaf N contents of the coffee plants in the wet season, but watering treatments applied in the dry season did not affect leaf N content.

Table 1. Effect of watering and fertilization treatments on relative soil water content (20 cm depth) and leaf nitrogen content of *Coffea arabica* (means±SD, $n = 5$). The data in parentheses are the percentages accounted for field water-holding capacity. HF: high fertilization, LF: low fertilization, M: rice straw mulch, I: drip irrigation, MI: mulch plus drip irrigation, CK: control (bare soil). *Measured in May 2002. The different letters represent statistical significance between means for each parameter within each treatment ($p<0.05$).

Treatment		RWC [%] Dry season	Wet season	Leaf N [%]
HF	M	16.2±0.5 (70.0) b	22.1±0.3 (96.7) a	3.11±0.23 a
	I	18.8±0.6 (72.7) b	22.7±1.4 (98.3) a	3.15±0.09 a
	MI	22.7±1.1 (98.2) a	23.8±0.4 (103.0) a	3.17±0.16 a
	CK	13.3±0.7 (57.5) c	22.9±1.1 (99.1) a	3.14±0.21a
LF	M	14.5±0.9 (63.0)bc	22.3±0.7 (96.5) a	2.48±0.24 b
	I	16.8±0.2 (72.7) b	22.5±2.1 (97.4) a	2.50±0.21 b
	MI	22.1±1.5 (95.7) a	22.4±0.3 (97.0) a	2.54±0.17 b
	CK	13.6±0.6 (58.8) c	21.9±1.0 (95.0) a	2.34±0.31 b

Vegetative growth: The height and lateral branch length growth rates of all the monitored coffee plants showed two clear peaks during the course of the study year under all of the watering and fertilization treatments (Fig. 2). The first highest growth peak appeared in May and the second one in August and September. At two growth peaks, the high fertilization group had significantly higher relative growth rate (RGR) of height and length of lateral branch than those of the low fertilization group ($p<0.01$), while no difference was found in the RGR of shoot numbers (*i.e*. the sprouting of new shoots) between

the two fertilization groups. Watering treatments slightly increased the height and branch length RGR of coffee plants in both the low and high fertilization groups, with mulching plus drip irrigation having the strongest effect, and mulching or drip irrigation having similar effects.

Photosynthesis: P_N in leaves of the coffee plants in the dry season was significantly lower than that in the wet season for all treatments (p<0.01). In the dry season, P_N values of the high-fertilization group were somewhat higher than those of the low-fertilization group, but no significant differences were found. Within fertilization groups, the watering treatments mulching, drip irrigation, and mulching plus drip irrigation increased P_N by 24.1–56.0 %, g_s by 7.1–28.6 %, E by 5.0–36.8 %, and water use efficiency (WUE) by 13.3–30.8 % (P_N/E). However, the effects of various watering treatments on the gas exchange parameters in the dry season did not continue throughout the wet season. High fertilization increased P_N (p<0.01) in the wet season, but had no effects on g_s, E, or WUE (all comparisons, p>0.05) (Table 2). The predawn values of the initial photochemical efficiency (F_v/F_m) in leaves of the coffee plants ranged from 0.82 to 0.85 and there were no significant differences in this parameter among treatments. The actual photochemical efficiency ($\Delta F_v'/F_m'$) and thermal energy dissipation efficiency estimated from the photochemical reflectance index (ΔPRI) were significantly higher in the wet season than the corresponding efficiencies in the dry season (two t-tests, each p<0.05). Watering treatments had no effects on the photochemical parameters, while high fertilization significantly reduced diurnal photoinhibition and increased both $\Delta F_v'/F_m'$ and ΔPRI (Table 3).

Table 2. Effect of watering and fertilization treatments on the gas exchange parameters in leaves of *C. arabica.* HF: high fertilization, LF: low fertilization; M: rice straw mulch; DS: dry season, WS: wet season; P_N: net photosynthetic rate, g_s: stomatal conductance, E: rate of transpiration, WUE: water use efficiency. The abbreviations for the watering treatments are as defined in Table 1.

Treatment		P_N [μmol m^{-2} s^{-1}]		g_s [mmol m^{-2} s^{-1}]		E [mmol m^{-2} s^{-1}]		WUE [mmol mol^{-1}]	
		DS	WS	DS	WS	DS	WS	DS	WS
HF	M	3.6 b	5.7 a	0.091 b	0.118 a	2.1 b	2.6 a	1.7 ab	2.2 a
	I	3.8 ab	5.8 a	0.097 b	0.114 a	2.2 b	2.8 a	1.9 a	2.1 a
	MI	4.5 a	6.1 a	0.119 a	0.121 a	2.4 a	2.9 a	1.9 a	2.1 a
	CK	2.9 bc	5.5 ab	0.085 c	0.116 a	2.0 c	2.7 a	1.5 bc	2.0 a
LF	M	3.3 b	5.0 b	0.088 b	0.117 a	2.2 b	2.7 a	1.5 bc	1.8 b
	I	3.6 b	5.3 b	0.092 b	0.113 a	2.3 b	2.9 a	1.6 b	1.8 b
	MI	3.9 ab	5.4 ab	0.114 a	0.119 a	2.6 a	2.8 a	1.7 ab	1.9 ab
	CK	2.5 c	4.8 b	0.078 c	0.112 b	1.9 c	2.8 a	1.3 c	1.7 b

Table 3. Effect of watering and fertilization treatments on the potential and actual photochemical efficiency, diurnal photoinhibition, and thermal dissipation efficiency as estimated from leaf reflectance indices in leaves of *C. arabica*. The abbreviations for the watering treatments are as defined in Table 1.

Treatment		Predawn F_v/F_m		Day photoinhib. [%]		$\Delta F_v'/F_m'$		ΔPRI×100	
		DS	WS	DS	WS	DS	WS	DS	WS
HF	M	0.825 a	0.826 a	19.1 b	18.9 b	0.51 a	0.52 a	3.1 a	3.4 a
	I	0.823 a	0.831 a	18.9 b	18.1 b	0.52 a	0.55 a	3.5 a	3.6 a
	MI	0.832 a	0.843 a	18.5 b	17.8 b	0.53 a	0.57 a	3.5 a	3.7 a
	CK	0.829 a	0.828 a	21.4 ab	20.5 ab	0.48 ab	0.52 a	3.4 a	3.3 a
LF	M	0.827 a	0.831 a	23.1 a	22.7 a	0.46 b	0.47 b	2.7 b	2.8 b
	I	0.831 a	0.833 a	22.6 a	22.5 a	0.45 b	0.48 b	2.4 b	2.7 b
	MI	0.829 a	0.838 a	23.4 a	21.8 ab	0.48 ab	0.49 ab	2.8 ab	2.9 b
	CK	0.819 b	0.828 a	24.2 a	23.5 a	0.45 b	0.46 b	2.3 b	2.6 b

Table 4. Results of two-way ANOVA for some physiological parameters of *C. arabica* in the dry season. ns: no significant difference (p>0.05), $^{*}p$<0.05, $^{**}p$<0.01.

	Source of variation		
	Water	Fertilization	W×F
Net photosynthetic rate (P_N)	**	*	*
Stomatal conductance (g_s)	**	ns	ns
Transpiration rate (E)	*	ns	ns
Water use efficiency (WUE)	**	*	*
% diurnal photoinhibition	ns	*	ns
$\Delta F_v'/F_m'$	ns	*	ns
ΔPRI	ns	*	ns

The two-way ANOVA for the photosynthetic parameters in the dry season showed that the watering treatments had significant effects on the gas exchange parameters, while the photochemical parameters were only affected by fertilization (Table 4). The interaction effects on P_N and WUE of the fertilization and watering treatments in the dry season were significant.

Discussion

The lowest N content in leaves of our studied coffee plants was 2.34 %, higher than the nutrient deficit thresholds reported by various authors (Barros *et al*. 1995, Müller 1996), indicating that both fertilization levels provided well-balanced nutrition for the coffee plants in our study. In the dry season, the lowest soil water content of bare soil in coffee plantation was around 57 % of the field water-holding capacity (Table 1), which is regarded as a moderate drought level for coffee plants (Da Matta *et al*. 1997, 2002, 2003, Cai *et al*. 2005).

In most coffee plantations worldwide, vegetative growth of coffee trees shows active and quiescent growth phases modulated by the local duration of conductive growing conditions (Da Matta *et al*. 1999). During the growth period in the monitored year, the coffee plants showed two growth peaks in the wet season (Fig. 2). The fertilization and watering treatments did not change this basic growth rhythm of coffee, implying that it is controlled by intrinsic rather than extrinsic abiotic factors, at least within the tested range of environmental conditions. Crops are often subjected to periods of water shortage, which ultimately lead to reduced growth and productivity. Biochemical constraints may limit photosynthetic CO_2 fixation directly when plants are subject to severe drought, while photosynthesis reductions are mainly due to stomatal limitations in moderate water deficit conditions (Lawlor and Cornic 2002). The reductions in g_s observed in coffee plants grown under the control conditions, compared to those grown under the mulched or irrigated conditions (Table 2), appear to reflect avoidance mechanisms that minimize water loss. Such responses have previously been observed in coffee seedlings (Da Matta *et al*. 1997, Cai *et al*. 2005).

The pre-dawn F_v/F_m ratios (0.82–0.85) in leaves of all coffee plants approached values (0.83) reported for healthy, unstressed C_3 plants (Demmig-Adams and Adams 1992), indicating that no photo-damage to PS2 reaction centres or slowly relaxing excitation energy quenching mechanisms had been induced by environmental stress (Foyer *et al*. 1994). The lower P_N values observed in the control coffee plants than in the watered plants might have been due to a mechanism dependent on stomatal closure, rather than damage to PS2. Therefore, in our study, it is unlikely that PS2 photochemistry appreciably affected carbon gain, and diurnal photoinhibition may reflect down-regulation of photosynthesis (Demmig-Adams and Adams 1992) related to the maintenance of zeaxanthin contents or seasonal acclimation processes involving thylakoid lipids (Müller *et al*. 2001).

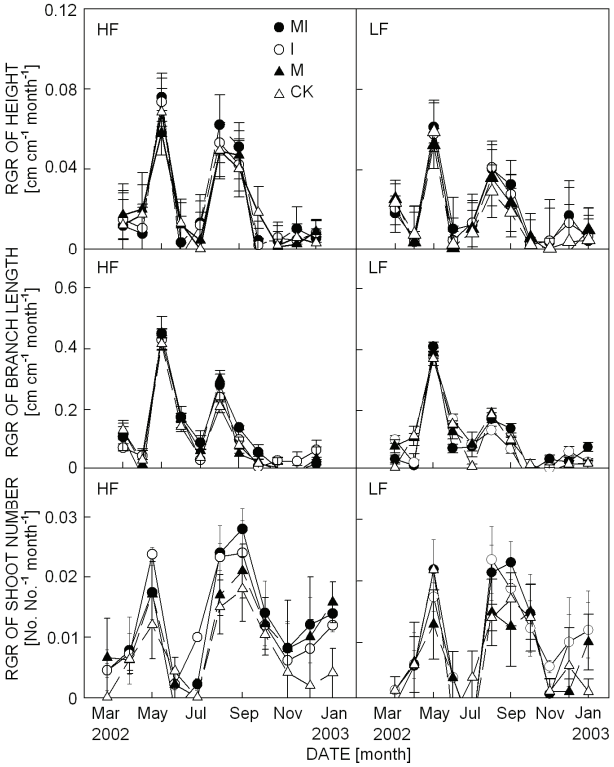

Fig. 2. Effects of watering and fertilization treatments on the relative growth rate (RGR) of the height, branch length, and shoot numbers of coffee plants. HF, high fertilization; LF, low fertilization. The abbreviations for the watering treatments are as defined in Table 1.

Photo-protection of PS2 was not achieved by an increase in non-radiative energy dissipation during drought conditions, because ΔPRI values did not differ significantly among the watering treatments in the dry season. Watering treatments, such as mulching and/or drip irrigation, had no significant effects on actual photochemical efficiency ($\Delta F_v'/F_m'$), diurnal thermal energy dissipation (ΔPRI), or diurnal photoinhibition of the coffee plants (Table 3), indicating that seasonal drought did not affect the 'internal' fluorescence characteristics of the plants.

High nutrient availability may either increase or decrease the g_s of plants (Lima *et al.* 1999, Livingston *et al*. 1999). In our study, high fertilization had a slight influence on g_s and E in the wet season (Table 2); the increase in P_N may be attributed to the improvement of the action of photosynthetic enzymes in coffee plants influenced by high fertilization. There were significant interaction effects of water and fertilization on the P_N and

WUE of the coffee plants, as previously found in controlled experiments in the laboratory and/or with pot-plants (Da Matta *et al*. 2002, Rahmana *et al*. 2005). High fertilization increased $\Delta F_v'/F_m'$ values and decreased the diurnal photoinhibition of the plants (Table 3), suggesting that high levels of nutrients increased the photochemical efficiency of coffee and alleviated diurnal photoinhibition, in accordance with the results of other studies (Da Matta *et al*. 2002, Dugald *et al*. 2003). Under restricted nutrient conditions, increases in the thermal energy dissipation of spinach (*Spinacia oleracea*) (Verhoeven *et al*. 1997), maize (Khamis *et al*. 1990), and eucalypt (*Eucalyptus nitens*) (Dugald *et al*. 2003) have been observed, but nutrient levels reportedly have no influence on the thermal energy dissipation of *Clematis vitalba*, at least within the ranges investigated by Bungard *et al*. (1997). In present study, the high ΔPRI values in the high fertilized coffee plants showed high nutrition would contribute to promoting of thermal energy dissipation capability and benefit coffee plants for adaptation under high-irradiance.

In conclusion, enhancement of the soil water content significantly promoted gas exchanges in leaves of coffee plants in the dry season, but had no influence on the internal fluorescence features of PS2. High-fertilized coffee plants have evolved the mechanism to acclimate to the high irradiance. The wet season is the optimal period for the photosynthetic carbon fixation and vegetative growth of coffee plants. Mulching and drip irrigation applied in the dry season have similar effects on vegetative growth and photosynthesis, but the former is more economical than the latter. Therefore, we recommend application of high levels of fertilization, together with straw mulching, in coffee plantations in Yunnan.

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