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Effects of irradiance on photosynthetic characteristics and growth of *Mosla chinensis* and *M. scabra*

J.-X. LIAO, Y. GE, C.-C. HUANG, J. ZHANG, Q.-X. LIU, and J. CHANG*

College of Life Science, State Key Laboratory of Plant Physiology and Biochemistry, Zhejiang University, Xixi campus, 232 Wensan Road, Hangzhou 310012, P.R. China

Abstract

Photosynthetic and growth characteristics of *Mosla chinensis* and *M. scabra* were compared at three irradiances similar to shaded forest understory, forest edge, and open land. At 25 % full ambient irradiance, *M. chinensis* and *M. scabra* had similar photosynthetic characteristics, but saturation irradiance, compensation irradiance, and apparent quantum yield of *M. chinensis* were higher than those of *M. scabra* at full ambient irradiance and 70 % full ambient irradiance. At the same irradiance treatment, specific leaf area and leaf area ratio of *M. chinensis* were lower than those of *M. scabra*. Photon-saturated photosynthetic rate and water use efficiency of *M. chinensis*, however, were not significantly higher than those of *M. scabra*, and the leaf area and total biomass were lower than those of *M. scabra*. As a sun-acclimated plant, the not enough high photosynthetic capacity and lower biomass accumulation may cause that *M. chinensis* has weak capability to extend its population and hence be concomitant in the community.

Additional key words: biomass accumulation; compensation and saturation irradiance; concomitant species; leaf area ratio; net photosynthetic rate; plasticity; specific leaf area; water use efficiency.

Introduction

Irradiance is one of the most important environmental factors affecting plant survival, growth, reproduction, and distribution. Plants grown at low irradiance (LI) often experience decreased ribulose-1,5-bisphosphate carboxylase/oxygenase activity and reduced net photosynthetic rate (P_N) and increased specific leaf area (SLA) and leaf area ratio (LAR) (Anderson 1986, Stitt and Schulze 1994, Kremer and Kropff 1999). In contrast to this, plants grown under high irradiance (HI) decrease their SLA due to extra layers of palisade or longer palisade cells (Vats *et al*. 2002). Besides, they absorb a large amount of photons and sustain high P_N and biomass (B) accumulation. A long time of high irradiance exposure, however, may damage the photosynthetic apparatus (Zhang *et al*. 2003). Thus, study on the photosynthetic and growth plasticity responses of plant to irradiance will contribute to the understanding of physiological mechanism of plant growth and distribution.

Mosla chinensis Maxim., an annual medicinal herb of the family Labiatae, is distributed in the south of Yangtze River drainage basin (Fang *et al.* 1989). The successful growth of *M. chinensis* is mainly restricted to gravel roadside or around the rock with ample sunlight but low water availability (Guan *et al.* 2003, 2004). In general, it is only the concomitant species in the community because it has a few individuals in each population (Guan *et al.* 2004). In contrast, *M. scabra* (Thunb.) C.Y. Wu *et* H.W. Li, a con-generic species of *M. chinensis* distributed widely in China, Japan, and Vietnam, is often dominant in the community. Its common habitat is restricted to shaded and moist conditions (Zhang and Xu 1988, Fang *et al.* 1989, Zhou 1999). Therefore a comparative study of photosynthetic and growth plasticity responses to three irradiances in *M. chinensis* and its common con-generic species *M. scabra* was conducted. The objective was to elucidate the relationship between photosynthetic and growth characteristics of the two species and irradiance and find out the reason why *M. chinensis* is often a concomitant species in the field from the point of view of plant eco-physiology.

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*Corresponding author; fax: (+86) 571 87972193, e-mail: jchang@mail.hz.zj.cn
Abbreviations: AQY – apparent quantum yield; B – total biomass; CI – compensation irradiance; *E* – transpiration rate; HI – high irradiance; LA – leaf area; LAR – leaf area ratio; LI – low irradiance; LMR – leaf mass ratio; MI – medium irradiance; P_{max} – photon-saturated photosynthetic rate; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; SI – saturation irradiance; SLA – specific leaf area; WUE – water use efficiency.
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Materials and methods

Plants and treatments: Research was conducted at the plantation of Zhejiang University, Hangzhou, eastern China (120º10'E, 30º15'N). Both *M. chinensis* and *M. scabra* were cultivated in pots (height 17 cm and diameter 15 cm) with a mixture of field soil and vermiculite (2 : 1, v/v) at the end of May 2003, after the seeds germinated and the seedlings had reached 5 cm. One week later, they were transferred to three different irradiances: high irradiance, HI (full ambient irradiance), medium irradiance, MI (70 % full ambient irradiance), and low irradiance, LI (25 % full ambient irradiance). They were controlled by different layers of nylon-net shade (placed at 2 m above ground) and corresponded to the irradiances at the open land, forest edge, and forest understory, respectively. The seedlings were irrigated at regular periods depending on weather and soil moisture status. Each treatment had three repetitions.

Measurements were conducted at the vigorous vegetation growth period (mid-July). P_N-PPFD response curves were measured using a portable gas exchange system (model *LCA-4*, *ADC*, Hoddesdon, UK) in the morning when there was no cloud. CO_2 and air temperature in the leaf chamber were maintained at 360 µmol mol^{-1} and 25 °C, respectively. PPFD started at 1 500 µmol m^{-2} s^{-1} and decreased stepwise to 0 µmol m^{-2} s^{-1}. Apparent quantum yield (AQY) was calculated from the initial slopes by linear regression using PPFD values below 200 µmol m^{-2} s^{-1}. Compensation irradiance (CI), saturation irradiance (SI), and PPFD-saturated P_N (P_{max}) were estimated. Leaf water use efficiency (WUE) was calculated using instantaneous values of P_N and transpiration rate (*E*), which were measured in the morning at the irradiance under which the plant was growing. After photosynthetic measurements, six individuals of each species were harvested from the three replication pots. Leaf area (LA) was measured using a portable leaf area meter (*Li-Cor-3000*, Lincoln, NE, USA). Then all samples were dried in an oven at 80 °C for at least 72 h. LA per unit leaf mass (specific leaf area, SLA), LA per unit of total mass (leaf area ratio, LAR), and leaf mass per unit of total mass (leaf mass ratio, LMR) were determined (Hunt 1978). Plasticity index was calculated for each variable and species according to Valladares *et al*. (2000) as the difference between the minimum and the maximum mean values among the three irradiances divided by the maximum mean value.

Statistical analysis: Standard error (SE) was calculated and differences in mean values of P_{max}, AQY, SI, CI, WUE, and LA, B, SLA, LAR, and LMR for each treatment between *M. chinensis* and *M. scabra* were tested at $p<0.05$ according to least significant difference (LSD).

Results

***P*$_N$-PPFD response under different growth irradiances** (Fig. 1): From 0 to 250 µmol m^{-2} s^{-1}, all the curves responded rapidly. After a while, the curves were gradually at a plateau. For both *Mosla* species, P_{max}, SI, and CI increased as growth irradiance increased, but the differences in P_{max} between HI and MI were not significant (Table 1). At the same growth irradiance, the differences in P_{max} between species were not significant**.** SI and CI for *M. chinensis* were significantly higher than those of *M. scabra* under HI and MI growth, while no difference was found under LI growth.

For *M. chinensis*, AQY were significantly higher under HI and MI than that under LI, but the differences between HI and MI were not significant. In *M. scabra*, AQY did not significantly differ between HI and LI growth, but AQY was significantly higher under MI. At the HI growth condition, AQY of *M. chinensis* was significantly higher than that of *M. scabra*, but there were no inter-specific differences at MI and LI.

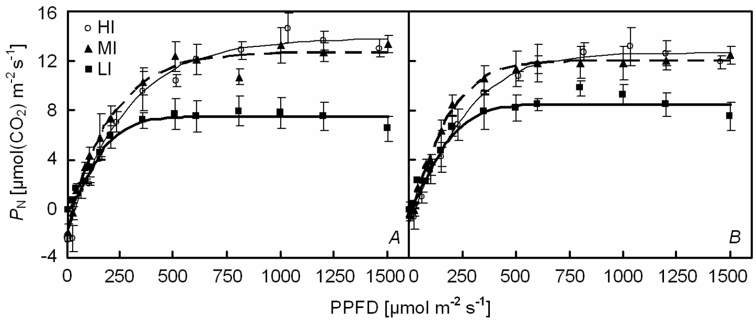

Fig. 1. Photosynthetic photon flux density (PPFD) response curves of net photosynthetic rate (P_N) of *M. chinensis* (*A*) and *M. scabra* (*B*) grown under high (HI, full ambient), medium (MI, 70 % full ambient), and low (LI, 25 % full ambient) irradiance. P_N was measured at CO_2 concentration of 360 µmol mol^{-1}, temperature of 25 °C, and PPFD of 0–1 500 µmol m^{-2} s^{-1}. Means ± SE of three replicates.

Table 1. Comparison of photosynthetic characteristics (P_{max}, photon-saturated photosynthetic rate; AQY, apparent quantum yield; SI, saturation irradiance; CI, compensation irradiance) of *M. chinensis* and *M. scabra* grown under high (HI, full ambient), medium (MI, 70 % ambient), and low (LI, 25 % ambient) irradiances. Means ± SE of three replicates. *Different letters* in each column indicate significant differences (p<0.05) between growth irradiances in the same species; *indicates significant difference between species at the same treatment (p<0.05).

Species	Growth irradiance	P_{max} [μmol(CO_2) m^{-2} s^{-1}]	AQY [mol mol^{-1}]	SI [μmol m^{-2} s^{-1}]	CI [μmol m^{-2} s^{-1}]
M. chinensis	HI	13.88±1.45^{a}	0.043±0.003^{a}	1046.82±24.86^{a}	31.13±2.10^{a}
	MI	12.78±1.61^{a}	0.045±0.003^{a}	745.07±36.01^{b}	19.15±2.44^{b}
	LI	7.53±1.04^{b}	0.029±0.002^{b}	540.81±29.14^{c}	3.64±1.86^{c}
M. scabra	HI	12.71±1.23^{a}	0.036±0.002^{b}*	903.60±36.76^{a}*	21.64±2.68^{a}*
	MI	12.05±1.17^{a}	0.045±0.004^{a}	656.36±39.24^{b}*	13.41±2.37^{b}*
	LI	8.53±0.98^{b}	0.032±0.002^{b}	519.87±13.98^{c}	2.72±1.59^{c}

Table 2. Comparison of growth traits (LA – leaf area; B – total biomass; SLA – specific leaf area; LAR – leaf area ratio; LMR – leaf mass ratio) of *M. chinensis* and *M. scabra* grown under high (HI, full ambient), medium (MI, 70 % ambient), and low (LI, 25 % ambient) irradiances. Means ± SE of six replicates. *Different letters* in each column indicate significant differences (p<0.05) between growth irradiances in the same species; *indicates significant difference between species at the same treatment (p<0.05).

Species	Growth irradiance	LA [cm^2]	B [g]	SLA [m^2 kg^{-1}]	LAR [m^2 kg^{-1}]	LMR [kg kg^{-1}]
M. chinensis	HI	113.34±20.199^{b}	2.96±0.49^{a}	10.33±1.47^{b}	3.83±0.50^{b}	0.37±0.07^{a}
	MI	191.34±24.64^{a}	2.40±0.52^{a}	18.82±1.39^{a}	7.96±1.00^{a}	0.42±0.08^{a}
	LI	88.11±19.15^{c}	1.05±0.33^{b}	19.29±1.57^{a}	8.37±0.88^{a}	0.43±0.09^{a}
M. scabra	HI	173.62±21.93^{b*}	3.28±0.52^{a}	14.17±1.40^{c*}	5.29±0.73^{c*}	0.37±0.07^{a}
	MI	247.35±26.74^{a*}	3.08±0.49^{a*}	19.95±2.15^{b}	8.03±1.31^{b}	0.40±0.08^{a}
	LI	179.19±25.36^{b*}	1.81±0.48^{b*}	24.02±1.71^{a*}	9.90±1.38^{a*}	0.41±0.08^{a}

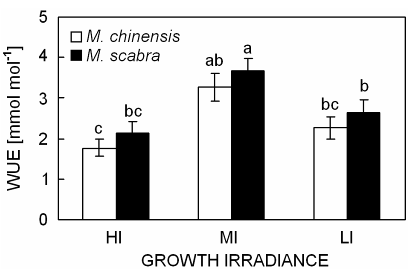

Fig. 2. Water use efficiency (WUE) determined at the irradiance under which plant was growing for *M. chinensis* and *M. scabra* grown under high (HI), medium (MI), and low (LI) irradiances. Means ± SE of three replicates. *Different letters* indicate significant differences (p<0.05).

Growth traits under different growth irradiances: For both species, LA was the largest at MI (Table 2). At the same irradiance, LA of *M. chinensis* was significantly smaller than that of *M. scabra*. B of both species responded similarly to irradiance. B at LI was significantly smaller than that at HI and MI. At the MI and LI growth, B of *M. chinensis* was significantly smaller than that of *M. scabra*, while no difference was found at HI growth.

SLA and LAR of both species decreased with an increase in photon availability and there were a significant difference between HI and LI. At HI and LI, SLA and LAR for *M. chinensis* were significantly lower than those of *M. scabra*, but there were no differences at MI. LMR, however, did not differ among the irradiances and the species.

Table 3. Plasticity index for each of physiological and growth traits in *M. chinensis* and *M. scabra*. P_{max}, AQY, SI, and CI are the same as in Table 1; LA, B, SLA, LAR, and LMR are the same as in Table 2; WUE – water use efficiency.

Traits	*M. chinensis*	*M. scabra*
P_{max} [μmol(CO_2) m^{-2} s^{-1}]	0.46	0.33
SI [μmol m^{-2} s^{-1}]	0.48	0.42
CI [μmol m^{-2} s^{-1}]	0.88	0.87
AQY [mol mol^{-1}]	0.34	0.28
LA [cm^2]	0.54	0.30
B [g]	0.64	0.45
SLA [m^2 kg^{-1}]	0.46	0.41
LAR [m^2 kg^{-1}]	0.54	0.47
LMR [kg kg^{-1}]	0.15	0.09
WUE [mmol mol^{-1}]	0.46	0.42

WUE under different growth irradiances: When WUE was measured at the irradiance under which the plant was growing, leaves of both species grown at MI had the greatest WUE (Fig. 2). At the same irradiance, WUE did not differ between *M. chinensis* and *M. scabra*.

Plasticity indices of *M. chinensis* and *M. scabra*: Among the traits, plasticity index for CI was the greatest, and that for LMR was the lowest. All plasticity indices of *M. chinensis* were higher than those of *M. scabra*, and the largest difference occurred in LAR, the smallest difference occurred in CI (Table 3).

Discussion

Xu and Shen (1998) suggested that plants grown at LI for a long time had lesser contents of electron transfer components and photosynthetic enzymes in comparison with plants grown at HI, which caused the P_{max} decrease. SI and CI are the important traits for photon energy utilization capability, whose declines are thought to adapt to LI. SLA and LAR are also very plastic growth traits which are strongly affected by photon supply (Jeangros and Nösberger 1992). Decreasing irradiances cause the increase of SLA and LAR with the result that photon capture by the leaves is increased (Semb 1996). In present study, irradiance strongly affected photosynthetic and growth characteristics of *M. chinensis* and *M. scabra,* plants grown at lower irradiances had lower P_{max}, SI, CI, and B and higher SLA and LAR.

Growing at 25 % full ambient irradiance, *M. chinensis* and *M. scabra* had similar photosynthetic characteristics, but SI, CI, and AQY of *M. chinensis* were higher than those of *M. scabra* at HI and MI (Table 1). This was consistent with the ample sunlight in the natural habitat of *M. chinensis* and the shade and moist condition for *M. scabra* (Zhang and Xu 1988, Fang *et al.* 1989, Zhou 1999).

At the same irradiance treatment, SLA and LAR of *M. chinensis* were lower than those of *M. scabra* (Table 2). P_{max} of *M. chinensis*, however, was not significant higher than *M. scabra* at all irradiances (Table 1), and its B was lower than that of *M. scabra* due to smaller LA (Table 2). This suggests that *M. chinensis*, a sun-acclimated plant, had a not enough high photosynthetic capacity and biomass accumulation and these may be the main reasons for its concomitance in the community.

Higher WUE may have contributed to the change of the photosynthetic apparatus (Mulkey and Pearcy 1992, Chazdon *et al*. 1996), and it is beneficial to plants grown in water-limited environments. According to WUE in this study and the above analysis, 70 % of full ambient irradiance habitat (roadside or forest edge) could be considered as the optimizing condition for sun-acclimated plant of *M. chinensis* and shade-acclimated plant of *M. scabra* that adapts to a more shade environment.

The higher plasticity indices of *M. chinensis* for photosynthetic and growth traits compared with those of *M. scabra* was consistent with the hypothesis that the sun-acclimated species has greater plasticity than shade-acclimated species (Lortie and Aarssen 1996, Valladares *et al*. 2000). In all plasticity indices, CI was the most sensitive trait in adapting to the changing irradiance. Kremer and Kropff (1999) suggested that LMR quantifies the fraction of total dry matter of a plant invested in leaves. In our study, however, irradiance did not significantly affect LMA of *M. chinensis* and *M. scabra*.

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