BRIEF COMMUNICATION

Photosynthetic characteristics and growth of *Mosla hangchowensis* and *M. dianthera* under different irradiances

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Abstract

The photosynthetic and growth characteristics of *Mosla hangchowensis*, an endangered species and *M. dianthera*, a weed, were compared under three irradiances (PPFD) similar to shaded forest understory, forest edge and open land. Both species grown at lower PPFD had lower PPFD-saturated photosynthetic rate (P_{max}), saturation PPFD, compensation PPFD, apparent quantum yield, total mass and root/shoot ratio and higher specific leaf area, leaf area ratio and height ratio. At the same PPFD treatment, however, specific leaf area and leaf area ratio of *M. hangchowensis* were higher than those of *M. dianthera*, other above parameters were lower than those of *M. dianthera*. Water use efficiency did not differ between *M. hangchowensis* and *M. dianthera*, but it reached its maximum at 70 % of full PPFD. These results suggested the optimum habitat of *M. hangchowensis* is the forest edge.

Additional key words: apparent quantum yield, net photosynthetic rate, radiant energy utilization, root/shoot ratio, water use efficiency.

Many physiological processes in plants are affected by irradiance, which is one of the most important environmental factors affecting plant survival, growth, reproduction and distribution (Smith 1982, Zhou 1999, Guan *et al*. 2002, Muraoka *et al*. 2002, Keller and Lüttge 2005). Plants grown in low photosynthetic photon flux density (PPFD) have lower net photosynthetic rate (P_N) and higher specific leaf area (SLA) and these two parameters affect the productivity of a plant (Anderson 1986, Stitt and Schulze 1994). In contrast to this, plants grown under high PPFD 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 accumulation. A long time of high PPFD exposure, however, may damage the photosynthetic apparatus (Zhang *et al*. 2003). Thus, study on the photosynthetic and growth responses of plant, especially endangered plant, to PPFD, will contribute to increase the understanding of physiological mechanism of plant distributions and assist in the development of approaches to conserve endangered species.

As an endemic annual plant in China, *M. hangchowensis* has only 5 small local populations, which were found along the coast in subtropical zone of China. It has been endangered distribution due to human activities (Ge and Chang 2001). In contrast, *M. dianthera* is distributed widely in most area in subtropical and tropical zone of China and other countries of East and Southeast Asia. From the field ecological studies, we found that the habitats of both species are open land, forest edge and forest understory, but *M. hangchowensis* have high mortality rate in open land habitat and most of individuals cannot live until fruiting period in the under forest habitat (Ge *et al*. 1999, Zhou 1999). These strongly suggest that PPFD may be important. In this study, a comparative study of photosynthesis and growth of *M. hangchowensis* and *M. dianthera* under different PPFD has been conducted.

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Abbreviations: AQY - apparent quantum yield; E - transpiration rate; LAR - leaf area ratio; LMR - leaf mass ratio; PAR - photosynthetically active radiation; P_{max} - PPFD-saturated photosynthetic rate; P_N - net photosynthetic rate; PPFD - photosynthetic photon flux density; R/S - root shoot ratio; SLA - specific leaf area; WUE - water use efficiency.
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Research was conducted at the plantation of Zhejiang University, Hangzhou, eastern China (120º10'E, 30º15'N). Both *M. hangchowensis* and *M. dianthera* 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 environments: high PPFD (full ambient PPFD), medium PPFD (about 70 % full ambient PPFD) and low PPFD (about 25 % full ambient PPFD), which were controlled by different layers of nylon-net shade (placed at 2 m above ground) and corresponded to the PPFD at the open land, forest edge and forest understory in the natural habitat, respectively. The seedlings were irrigated at regular periods depending on the weather and soil moisture status and each treatment had three repetitions.

Measurements were conducted at the vigorous vegetation growth stage (mid July). PPFD response curves were measured using a portable gas exchange system (*Model LCA-4*, *ADC Ltd*., Hoddesdon, UK). Measurements were carried out in the morning when there was no cloud. CO_2 and air temperature in the leaf chamber was maintained at 360 μmol mol^{-1} and 25 °C, respectively. PPFD started at 1500 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 PPFD, saturation PPFD and PPFD-saturated photosynthetic rate (P_{max}) were estimated. Leaf water use efficiency (WUE) was calculated using instantaneous values of net photosynthetic rate (P_N) and transpiration rate (E), which were measured in the morning with the PPFD under which plant was growing. After photosynthetic measurements, six individuals of each species were harvested from the three replications pots. The height of the individuals was measured before harvest. All leaf area was determined 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. Leaf area per unit leaf mass (specific leaf area, SLA), leaf area per unit of total mass (leaf area ratio, LAR), leaf mass per unit of total mass (leaf mass ratio, LMR), height per unit of total mass (height ratio) and root mass / shoot mass (R/S ratio) were determined according to Hunt (1978).

Standard error (SE) was calculated and differences in mean values of above mentioned parameters for each treatment between *M. hangchowensis* and *M. dianthera* were tested at $P < 0.05$ according to least significant difference (LSD).

The response of P_N to PPFD in both species differed among growth PPFD (Fig. 1). When PPFD was < 300 μmol m^{-2} s^{-1}, all the plants responded rapidly. After a while, the curves were gradually at a plateau. At all measured PPFD, mean P_N of *M. hangchowensis* was lower than that of *M. dianthera* grown under high and medium PPFD, while no difference in those grown under low PPFD.

For both species, P_{max}, saturation PPFD, compensation PPFD and AQY were significantly higher under high and medium PPFD growth conditions than those under low PPFD growth condition (Table 1, Fig. 2*A*). At high and medium growth PPFD, these parameters for *M. hangchowensis* were significantly lower than in *M. dianthera*, which indicated the photosynthetic capacity and photosynthetically active radiation (PAR) utilization of *M. hangchowensis* were lower than those of *M. dianthera* because P_{max} is the capable of photosynthetic gain (on a leaf basis) (Barker *et al*. 1997) and saturation PPFD, compensation PPFD and AQY are positively correlated with PAR utilization (Harley and Baldocchi 1995, Davies 1998, Huante and Rincón 1998).

When measured at the PPFD under which plant was growing, WUE did not differ between *M. hangchowensis* and *M. dianthera*, but it reached its maximum at medium PPFD (Fig. 2*B*). Higher WUE is beneficial to plants grown in water-limited environments (Mulkey and Pearcy 1992). So 70 % full ambient PPFD growth environments could be considered as the optimum habitat for *M. hangchowensis* and *M. dianthera*.

SLA and LAR are very plastic growth traits, which are strongly affected by photon supply (Jeangros and Nösberger 1992). Decreasing PPFD cause the increase

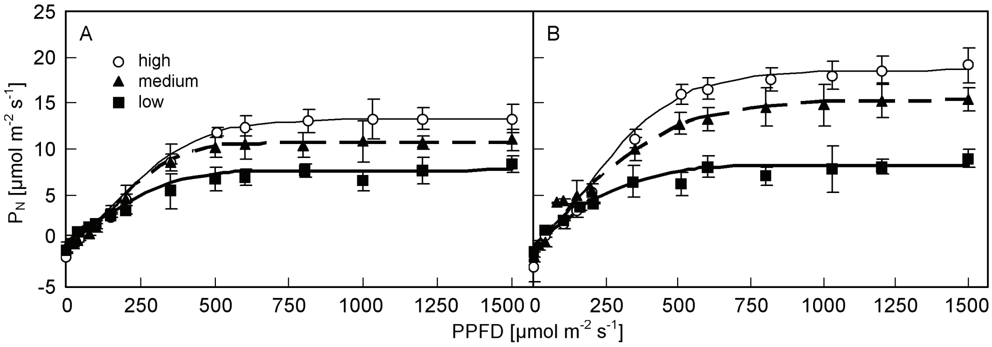

Fig. 1. Response of net photosynthetic rate (P_N) to PPFD in *M. hangchowensis* (*A*) and *M. dianthera* (*B*) grown under high (full ambient), medium (about 70 %) and low (about 25 %) PPFD. P_N were measured at CO_2 concentration of 360 μmol mol^{-1} and temperature of 25 °C, with photosynthetic photon flux density (PPFD) values ranging from 0 to 1500 μmol m^{-2} s^{-1}. Data are the means ± SE of three replicates.

Table 1. Comparison of photosynthetic characteristics of *M. hangchowensis* and *M. dianthera* grown under high, medium and low PPFD. P_{max} - PPFD-saturated photosynthetic rate. Data are the means ± SE of three replicates. Different letters in each column indicate significant differences (P < 0.05) between growth PPFD conditions in the same species; * indicates significant difference between species at the same treatment (P < 0.05).

Species	Growth PPFD	P_{max} [μmol m^{-2} s^{-1}]	Saturation PPFD [μmol m^{-2} s^{-1}]	Compensation PPFD [μmol m^{-2} s^{-1}]
M. hangchowensis	high	13.34 ± 1.61a	928.24 ± 13.98a	28.96 ± 4.97a
	medium	10.78 ± 1.15a	666.57 ± 29.75b	17.97 ± 3.37b
	low	7.69 ± 1.04b	533.47 ± 33.23c	3.43 ± 1.59c
M. dianthera	high	18.63 ± 1.43a*	1096.60 ± 56.01a*	40.73 ± 3.68a*
	medium	15.28 ± 1.52b*	975.52 ± 24.86b*	27.97 ± 2.10b*
	low	8.17 ± 0.98c	564.09 ± 29.14c	4.44 ± 1.86c

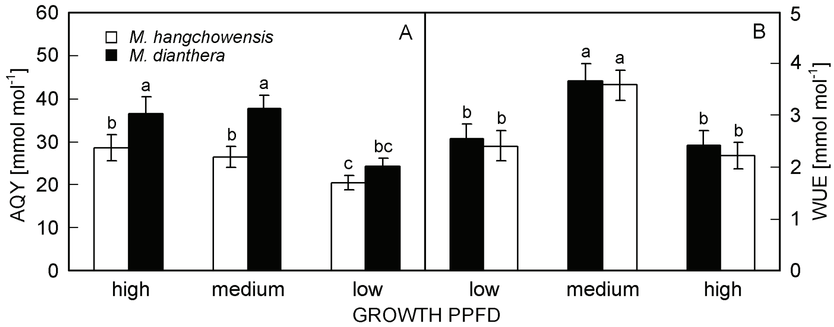

Fig. 2. Comparison of apparent quantum yield (AQY, *A*) and water use efficiency (WUE, *B*) of *M. hangchowensis* and *M. dianthera* grown under high, medium and low PPFD. Data are the means ± SE of three replicates. Different letters in each figure indicate significant differences (P < 0.05).

Table 2. Comparison of growth traits of *M. hangchowensis* and *M. dianthera* grown under high, medium and low PPFD. SLA - specific leaf area; LAR - leaf area ratio; LMR - leaf mass ratio; R/S - root/shoot ratio. Data are the means ± SE of six replicates. Different letters in each column indicate significant differences (P < 0.05) between growth PPFD conditions in the same species; * indicates significant difference between species at the same treatment (P < 0.05).

Species	Growth PPFD	Total mass [g]	SLA [cm^2 g^{-1}]	LAR [cm^2 g^{-1}]	Height ratio [cm g^{-1}]	LMR [g g^{-1}]	R/S
M. hangchowensis	high	3.05 ± 0.60a	123.80 ± 13.80b	49.52 ± 6.14b	11.28 ± 3.10b	0.40 ± 0.08a	0.33 ± 0.05a
	medium	2.86 ± 0.51a	191.81 ± 17.33a	79.81 ± 8.57a	14.43 ± 2.53b	0.42 ± 0.08a	0.26 ± 0.05b
	low	1.12 ± 0.40b	211.98 ± 18.70a	96.53 ± 16.40a	23.07 ± 4.16a	0.46 ± 0.09a	0.11 ± 0.02c
M. dianthera	high	3.15 ± 0.48a	100.57 ± 13.56b*	34.69 ± 4.96b*	21.59 ± 3.85c*	0.34 ± 0.07a	0.39 ± 0.06a*
	medium	2.59 ± 0.45a	184.78 ± 14.60a	72.75 ± 8.22a	35.57 ± 4.80b*	0.39 ± 0.08a	0.33 ± 0.06a*
	low	1.10 ± 0.33b	191.34 ± 12.78a*	77.48 ± 9.96a*	47.22 ± 4.97a*	0.40 ± 0.08a	0.12 ± 0.02b

of SLA and LAR with the result that PAR capture by the leaves are increased (Semb 1996). Significantly higher SLA and LAR in lower PPFD were found in *M. hangchowensis* and *M. dianthera*, but *M. hangchowensis* had higher SLA and LAR than those of *M. dianthera* (Table 2), which caused total mass of *M. hangchowensis* was similar to *M. dianthera* at the same growth PPFD condition due to lower photosynthetic rate per unit leaf area. *M. hangchowensis* had significantly lower height ratio than that of *M. dianthera* at all PPFD treatments (Table 2), meaning the competition for PAR of *M. hangchowensis* was lower than *M. dianthera* because higher height ratio means more competition for PAR when total mass is similar (Sakai 1995, Pothier and Prévost 2002). LMR quantifies the fraction of total dry matter of a plant invested in leaves (Kremer and Kropff 1999). During the present experiment, LMR did not change but the R/S increased with increasing growth PPFD (Table 2), implying a switch from investment in leaf biomass into investment in roots. Compared with *M. dianthera* at the same condition, the smaller R/S suggested that *M. hangchowensis* had lower nutrient and water absorptive capacity from soil.

In the field ecological studies, we found that the optimizing habitat of *M. hangchowensis* is the forest edge, which is few and dispersed and is disturbed by humans more and more frequently (Chang *et al*. 1999, Ge and Chang 2001). In the under forest habitat, *M. hangchowensis* had low photosynthetic capacity, PAR utilization, biomass accumulation and investment in roots, and died largely before fruiting period (Chang *et al*. 1999, Ge and Chang 2001). So *M. hangchowensis* now is mainly distributed in island-shaped soil on big, bare rocks or along the sunny side of hill peaks, *i.e.* open land habitat, which are abundant PPFD, thin soil and low water availability. According to above analysis, *M. hangchowensis* has significantly lower photosynthetic capacity, PAR utilization, competition for sunlight and investment in roots than *M. dianthera* at full sunlight growth environment. The contradictions between low water use efficiency and the low water availability in open land habitat may be the main cause why naturally occurring *M. hangchowensis* cannot recover easily if its environment is disturbed. Conversely, the higher photosynthesis, PAR utilization, competition for sunlight and investment in roots of *M. dianthera* are indicative of its success.

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