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Photosynthetic parameters of *Mosla hangchowensis* and *M. dianthera* as affected by soil moisture

Y. GE, Y.-J. LU, J.-X. LIAO, B.-H. GUAN, and J. CHANG*

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

Abstract

We compared the photosynthetic traits in response to soil water availability in an endangered plant species *Mosla hangchowensis* Matsuda and in a weed *Mosla dianthera* (Buch.-Ham.) Maxim. The highest diurnal mean net photosynthetic rate (P_{Nmean}), stomatal conductance (g_s), and water use efficiency (WUE) of both species occurred at 60 % soil water holding capacity (WHC), while the lowest values occurred at 20 % WHC. The P_{Nmean}, g_s, and chlorophyll (Chl) *a* and *b* contents of *M. hangchowensis* were lower than those of *M. dianthera*, while the physiological plasticity indices were higher than those of *M. dianthera*. *M. hangchowensis* had strong adaptability to the changing soil water status but weak extending population ability in its habitats because of the low P_{Nmean}, which may be one of the causes of its endangerment.

Additional key words: adaptation; chlorophyll content; endangered plant; net photosynthetic rate; stomatal conductance; transpiration rate; water use efficiency.

Introduction

Depending on environmental conditions, plants can alter their development, physiological process, and life history to adapt to changing environments, and take up plasticity variance (Via *et al*. 1995, Sultan 2001). Most plants may suffer water stress during their growth. In order to evade or decrease the influences of water stress, some plants adapt to the changing environment by altering photosynthetic characteristics and show environmental modification (Xu *et al*. 1995, Basu 1999, Mann and Wetzel 1999, Shangguan *et al*. 2000). This may contribute to the ability of species to occupy variable and diverse habitats in nature.

Both *Mosla hangchowensis* Matsuda and *M. dianthera* (Buch.-Ham.) Maxim. belong to the same genus of mint family (Labiatae), and the distribution overlaps. As an endemic annual plant in China, *M. hangchowensis* has only several small local populations, which were found along the coast in subtropical zone of China. It has been endangered because the number and distribution areas are decreasing quickly due to the recent human activities (Ge and Chang 2001). In contrast, the weed *M. dianthera* distributes widely in most areas of subtropical and tropical zone of China and other countries of East and Southeast Asia. In the field ecological studies, we found that the habitats of both species are thin soil on the rocks, hills, and roadside. Water stress appears frequently, so the soil water status is important (Ge *et al*. 1999, Zhou 1999). What is responsible for the difference in frequency of the two species? How does their physiology react to the changing soil water content? We compared photosynthesis in the two species, trying to elucidate the relationship between photosynthetic plasticity of the two species and soil water conditions and find out the reasons for the endangerment of *M. hangchowensis*.

Materials and methods

Plants and treatments: Research was conducted at the plantation of Zhejiang University, Hangzhou, southeast China (120º10'E, 30º15'N). Both *M. hangchowensis* and *M. dianthera* were grown in pots (height 17 cm and

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*Corresponding author; phone: (+86) 571 87972193, fax: (+86) 571 87972193, e-mail: jchang@mail.hz.zj.cn

Abbreviations: Chl – chlorophyll; *E* – transpiration rate; g_s – stomatal conductance; P_N – net photosynthetic rate of leaf; P_{Nmean} – diurnal mean photosynthetic rate per individual; W_{90}, W_{60}, W_{40}, W_{20} – soil water content at 90, 60, 40, and 20 % WHC, respectively; WHC – soil water holding capacity; WUE – water use efficiency (P_N/E).

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diameter 15 cm) at the end of May 2000, after the seeds germinated and the seedlings had reached 5 cm. One week later, four soil water treatments commenced and each treatment had ten repetitions. For the well-watered treatment (W_{90}), plants were watered to saturate when soil moisture dropped to 90 % water holding capacity (WHC). Similarly, for the mild, middle, and severe periodic drought, water was added to saturation when soil moisture dropped to 60 % (W_{60}), 40 % (W_{40}), and 20 % (W_{20}) WHC, respectively.

Measurements were conducted at the vigorous vegetation growth period of two species (mid-July). Net photosynthetic rate (P_N) was measured every hour from 06:00 to 19:00 by an infrared CO_2 analyzer (*GHX305A*, China-German Co-operation, Beijing, China) in a close system. Stomatal conductance (g_s) and transpiration rate (E) were measured using a portable steady-state porometer (*Li-1600*, *Li-Cor*, Lincoln, USA). Leaf water use efficiency (WUE) was calculated as P_N/E. Chlorophyll (Chl) was extracted using ethanol and ethane according to Peng and Liu (1992). The concentrations of Chl *a* and Chl *b* in extracts were determined from absorbances at 663 and 645 nm, respectively, with a *HP 751* spectrophotometer (*HP*, Shanghai, China). 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 four soil water treatments divided by the maximum mean value.

Statistical analysis: Standard error (SE) was calculated and differences in mean values of P_N, g_s, WUE, and Chl for each treatment between *M. hangchowensis* and *M. dianthera* were tested at $p<0.05$ according to least significant difference test (LSD).

Results

P_N under different soil water status displayed in both species a double-peaked diurnal curve at all treatments (Fig. 1). The midday depressions of *M. hangchowensis* occurred at about 15:00 for W_{60} and W_{40}, and at about 13:00 for W_{90} and W_{20}. The diurnal mean photosynthetic rate (P_{Nmean}) in W_{90} was higher than in W_{20} and W_{40}, but the difference between W_{90} and W_{60} was insignificant (Table 1). The photosynthesis depressions of *M. dianthera* occurred at about 15:00 for all treatments (Fig. 1*B*). P_{Nmean} in W_{60} and W_{40} were higher than in W_{20}, but there was no significant difference between W_{90} and other treatments (Table 1). At the same water treatment, the P_{Nmean} of *M. hangchowensis* was lower than in *M. dianthera*, which was significant at all treatments except W_{90}.

Table 1. Comparison of mean net photosynthetic rate (P_{Nmean}), chlorophyll (Chl) *a* and *b* contents, and Chl *a*/*b* of *M. hangchowensis* and *M. dianthera* under different soil water status. Means ± SE. *Different letters* in each column express significantly different results between soil water treatments in the same species (a, b, c) or between the species with the same treatment (A, B).

Species	Treatment	P_{Nmean} [μmol(CO_2) m^{-2} s^{-1}]	Chl *a* [g kg^{-1}(DM)]	Chl *b* [g kg^{-1}(DM)]	Chl *a*/*b*
M. hangchowensis	W_{90}	$8.31 \pm 2.75^{a/A}$	$2.64 \pm 0.16^{c/B}$	$0.72 \pm 0.05^{b/B}$	$3.66 \pm 0.16^{a/A}$
	W_{60}	$9.56 \pm 3.14^{a/B}$	$2.34 \pm 0.14^{cd/B}$	$0.62 \pm 0.04^{b/B}$	$3.75 \pm 0.17^{a/A}$
	W_{40}	$5.13 \pm 2.11^{b/B}$	$2.19 \pm 0.13^{d/B}$	$0.67 \pm 0.05^{b/B}$	$3.29 \pm 0.15^{b/A}$
	W_{20}	$4.21 \pm 2.84^{b/B}$	$2.01 \pm 0.12^{d/B}$	$0.69 \pm 0.05^{b/B}$	$2.92 \pm 0.16^{c/A}$
M. dianthera	W_{90}	$9.97 \pm 3.76^{ab/A}$	$5.31 \pm 0.19^{a/A}$	$2.15 \pm 0.15^{a/A}$	$2.47 \pm 0.11^{d/B}$
	W_{60}	$12.95 \pm 4.41^{a/A}$	$5.12 \pm 0.21^{ab/A}$	$2.22 \pm 0.16^{a/A}$	$2.31 \pm 0.10^{de/B}$
	W_{40}	$12.45 \pm 4.21^{a/A}$	$4.86 \pm 0.17^{b/A}$	$2.29 \pm 0.16^{a/A}$	$2.12 \pm 0.12^{e/B}$
	W_{20}	$7.27 \pm 4.27^{b/A}$	$4.47 \pm 0.18^{b/A}$	$2.32 \pm 0.16^{a/A}$	$1.93 \pm 0.11^{e/B}$

Stomatal conductance under different soil water status: The g_s values were measured in the morning (about 10:00) and afternoon (about 16:00) (Fig. 2). There was no prominent difference for *M. hangchowensis* between morning and afternoon at the same water treatment. However, g_s of *M. dianthera* in the morning was larger than in the afternoon at all water statuses. The responses of g_s of the two species to soil water were similar to that of P_{Nmean}. That is, g_s in W_{90} was higher than in W_{20} both in the morning and in the afternoon. There was no significant difference for *M. hangchowensis* at W_{90}, W_{60}, or W_{40}, while for *M. dianthera*, W_{60} and W_{40} were higher than W_{90} and W_{20} in the morning and afternoon. Compared with *M. dianthera*, g_s values of *M. hangchowensis* were lower at all water treatments, and the largest and the smallest difference occurred at W_{20} and W_{90}, respectively. The two species showed a similar pattern in which P_N increased gradually with g_s in W_{90} (Fig. 3). However, P_N of *M. hangchowensis* was enhanced more obviously by a slight increase of g_s than that of *M. dianthera*, which suggested that P_N of *M. hangchowensis* was more sensitive to g_s than that of *M. dianthera.*

WUE under different soil water status: In both *M. hangchowensis* or *M. dianthera* the largest and the smallest WUE occurred at W_{60} and W_{20}, respectively, but there were no significant differences among W_{60}, W_{90}, and W_{40}. At the same water status, the difference in WUE between *M. hangchowensis* and *M. dianthera* was not significant (Fig. 4).

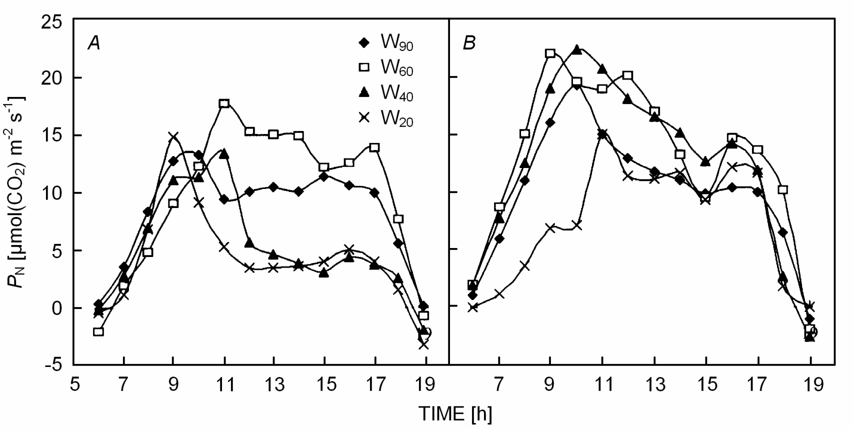

Fig. 1. Diurnal changes of net photosynthetic rate (P_N) of *M. hangchowensis* (*A*) and *M. dianthera* (*B*) grown under different soil moisture: W_{90}, W_{60}, W_{40}, W_{20}, respectively.

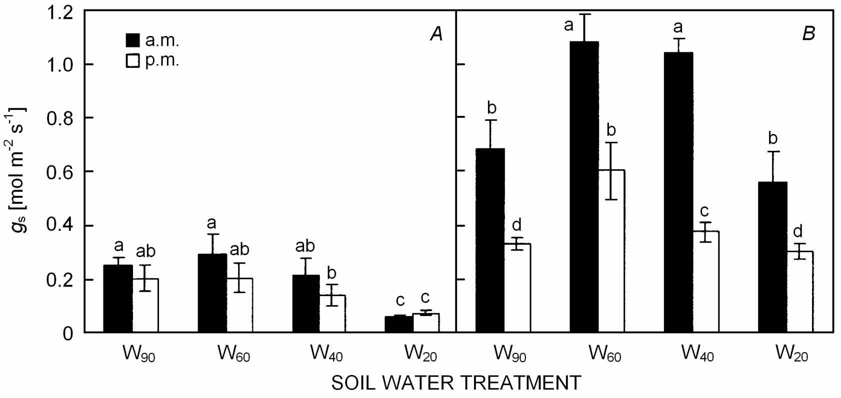

Fig. 2. Comparison of stomatal conductance (g_s) in the morning (a.m.) and in the afternoon (p.m.) of *M. hangchowensis* (*A*) and *M. dianthera* (*B*) grown under different soil water status. Means ± SE. *Different letters* in each figure express significantly different results between soil water treatments or between morning and afternoon with the same treatment in the same species. The inter-specific differences at the same treatment were significant.

Chl content under different soil water status: Content of Chl *a* of *M. hangchowensis* decreased with the increase of soil water stress and there were significant differences between W_{90} and W_{40}/W_{20} (Table 1). Soil water status did not affect Chl *b* content, so the Chl *a*/*b* ratio decreased with the decrease of soil water content. Under different soil water status, Chl *a*, Chl *b*, and Chl *a*/*b* in *M. dianthera* had similar trends as in *M. hangchowensis*. However, at the same soil water status, Chl *a* and Chl *b* contents of *M. dianthera* were larger than those of *M. hangchowensis*, and Chl *a*/*b* was smaller in *M. dianthera* (Table 1).

Plasticity indices of *M. hangchowensis* and *M. dianthera*: Plasticity index for g_s was the greatest followed by P_{Nmean}, and Chl *b* was the lowest (Table 2). All plasticity indices of *M. hangchowensis* were higher than those of *M. dianthera*, and the largest difference occurred in g_s in the morning; the smallest difference occurred in Chl *a*/*b*.

Discussion

Phenotypic plasticity plays an important role in plant adaptation to changing environments by buffering the effect of natural selection acting on genotypes (Bradshaw 1965, Schlichting 1986, Scheiner 1993, Dewitt *et al.*

1998). There were obvious physiological plasticities in *M. hangchowensis* and *M. dianthera* response to soil water status. Both species had the highest P_{Nmean}, g_s, and WUE at mild drought (W_{60}) but the lowest at severe drought (W_{20}). It suggested the two soil moistures might be optimum and stress-inducing for both *M. hangchowensis* and *M. dianthera*, respectively.

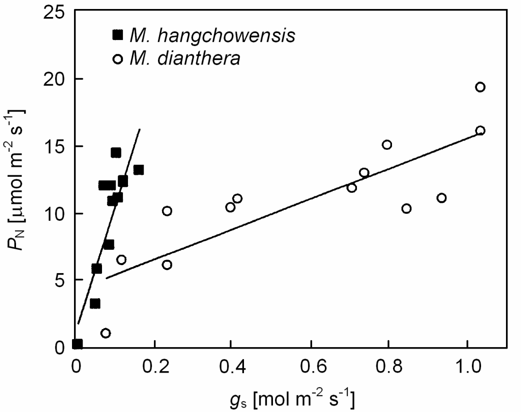

Fig. 3. Relationship between net photosynthetic rate (P_N) and stomatal conductance (g_s) of *M. hangchowensis* and *M. dianthera* at well-watered treatment (W_{90}).

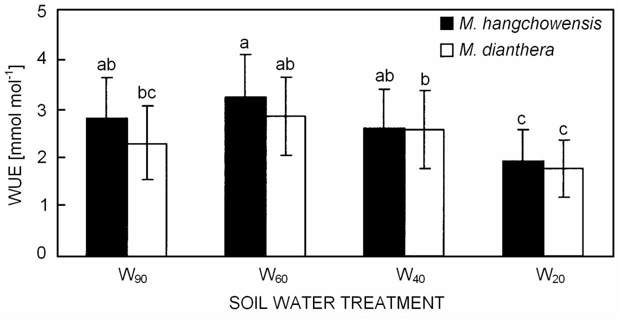

Fig. 4. Comparison of water use efficiency (WUE) of *M. hangchowensis* and *M. dianthera* grown under different soil water status. Means ± SE. *Different letters* express significantly different results between soil water treatments in the same species or between the species with the same treatment.

P_N correlated to g_s positively in *M. hangchowensis* and *M. dianthera* (Fig. 3) and the responses of P_{Nmean} to soil water status were similar to those of g_s. Hence the stomatal closure was one of the reasons for photosynthesis depression under drought. With the increase of soil water stress, Chl *a* decreased but Chl *b* did not change significantly (Table 1). Therefore, the decreased Chl *a* content was another reason for photosynthesis decrease under drought.

The Chl *a*/*b* ratio is generally higher in sun-acclimated leaves because these leaves have relatively less Chl associated with the light-harvesting-complex (which has a lower Chl *a*/*b*) than with the photosystems (Anderson 1986, Lambers *et al.* 1998). In the present study, Chl *a*/*b* of the two species was significantly lower at middle and severe periodic drought treatments (W_{40} and W_{20}) than at well-watered and mild periodic drought treatments (W_{90} and W_{60}). This implied the capacity of sun-acclimation of the two species decreased with the increase in soil water stress. At the same soil water status, the Chl *a*/*b* ratios of *M. hangchowensis* were higher but the Chl *a* and Chl *b* contents were lower than those of *M. dianthera*, which indicated the capacity of acclimation to high irradiance of *M. hangchowensis* was stronger than that of *M. dianthera*.

By comparing plasticity indices of physiological traits in *M. hangchowensis* and *M. dianthera*, we found the plasticity in g_s was the greatest response to soil water status and the inter-specific variation in plasticity was also largest for g_s (Table 2). That suggests the stomatal regulation is the important mechanism for the two species to adapt to changing soil water conditions, and the stomata of *M. hangchowensis* are more sensitive to soil water change than those of *M. dianthera*. However, there was no significant difference in WUE between the two species, even though g_s of *M. hangchowensis* was significantly lower than that of *M. dianthera* at the same water treatment, which indicated stomatal regulation of *M. hangchowensis* was at the cost of lower photosynthesis.

Table 2. Plasticity index for each of physiological parameters in *M. hangchowensis* and *M. dianthera*.

Parameters	*M. hangchowensis*	*M. dianthera*
P_{Nmean} [μmol(CO$_2$) m^{-2} s^{-1}]	0.56	0.44
g_s (a.m.) [mol m^{-2} s^{-1}]	0.79	0.48
g_s (p.m.) [mol m^{-2} s^{-1}]	0.63	0.50
WUE [mmol mol^{-1}]	0.41	0.38
Chl *a* [g kg^{-1}(DM)]	0.24	0.16
Chl *b* [g kg^{-1}(DM)]	0.14	0.07
Chl *a*/*b*	0.23	0.21

Low growth rate is advantageous for plant survival (Fenner 1978, Gross 1984). According to Chang *et al.* (1999) and our study, *M. hangchowensis* grows slowly and decreases photosynthesis under drought condition, which may enable it to survive under temporal drought but does not stimulate the extension of population. *M. dianthera* has lower plasticity than *M. hangchowensis* (Table 2), but its higher photosynthetic capacity causes its stronger capability to extend its population than *M. hangchowensis*. Therefore, *M. hangchowensis* pays out more cost for higher plasticity and the weak extending population capability because lower P_N may be one of the reasons of its endangerment.

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