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

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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 ($P_{\text{Nmean}}$), 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 $P_{\text{Nmean}}$, $g_s$, 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 $P_{\text{Nmean}}$, 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 (120°10’E, 30°15’N). Both *M. hangchowensis* and *M. dianthera* were grown in pots (height 17 cm and...
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 (W90), 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% (W60), 40% (W40), and 20% (W20) WHC, respectively.

Measurements were conducted at the vigorous vegetation growth period of two species (mid-July). Net photosynthetic rate (PN) was measured every hour from 06:00 to 19:00 by an infrared CO2 analyzer (GH1305A, China-German Co-operation, Beijing, China) in a close system. Stomatal conductance (gs) and transpiration rate (E) were measured using a portable steady-state porometer (GHX305, China-German Co-operation, Beijing, China) in a close system. The midday depressions of species a double-peaked diurnal curve at all treatments occurred at about 15:00 for W60 and W40, and at about 13:00 for W20 and W0. The diurnal mean photosynthetic rate (PNmean) in W90 was higher than in W20 and W40, but the difference between W90 and W20 was insignificant (Table 1). The photosynthesis depressions of M. dianthera occurred at about 15:00 for all treatments (Fig. 1B). PNmean in W60 and W40 were higher than in W20, but there was no significant difference between W90 and other treatments (Table 1). At the same water treatment, the PNmean of M. hangchowensis was lower than in M. dianthera, which was significant at all treatments except W60.

Results

PN 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 W90 and W40, and at about 13:00 for W60 and W20. The diurnal mean photosynthetic rate (PNmean) in W90 was higher than in W20 and W40, but the difference between W90 and W20 was insignificant (Table 1). The photosynthesis depressions of M. dianthera occurred at about 15:00 for all treatments (Fig. 1B). PNmean in W60 and W40 were higher than in W20, but there was no significant difference between W90 and other treatments (Table 1). At the same water treatment, the PNmean of M. hangchowensis was lower than in M. dianthera, which was significant at all treatments except W60.

Table 1. Comparison of mean net photosynthetic rate (PNmean), 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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>PNmean [µmol(CO2) m2 s-1]</th>
<th>Chl a [g kg⁻¹(DM)]</th>
<th>Chl b [g kg⁻¹(DM)]</th>
<th>Chl a/b</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. hangchowensis</td>
<td>W90</td>
<td>8.31 ± 2.75±A</td>
<td>2.64 ± 0.16±B</td>
<td>0.72 ± 0.0±b</td>
<td>3.66 ± 0.16±A</td>
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<td></td>
<td>W60</td>
<td>9.56 ± 3.14±B</td>
<td>2.34 ± 0.14±B</td>
<td>0.62 ± 0.0±b</td>
<td>3.75 ± 0.17±A</td>
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<tr>
<td></td>
<td>W40</td>
<td>5.13 ± 2.11±B</td>
<td>2.19 ± 0.13±B</td>
<td>0.67 ± 0.0±b</td>
<td>3.29 ± 0.15±A</td>
</tr>
<tr>
<td></td>
<td>W20</td>
<td>4.21 ± 2.84±B</td>
<td>2.01 ± 0.12±B</td>
<td>0.69 ± 0.0±b</td>
<td>2.92 ± 0.16±A</td>
</tr>
<tr>
<td>M. dianthera</td>
<td>W90</td>
<td>9.97 ± 3.76±A</td>
<td>5.31 ± 0.19±A</td>
<td>2.15 ± 0.19±A</td>
<td>2.47 ± 0.11±B</td>
</tr>
<tr>
<td></td>
<td>W60</td>
<td>12.95 ± 4.41±A</td>
<td>5.12 ± 0.21±A</td>
<td>2.22 ± 0.16±A</td>
<td>2.31 ± 0.10±cB</td>
</tr>
<tr>
<td></td>
<td>W40</td>
<td>12.45 ± 4.21±A</td>
<td>4.86 ± 0.17±A</td>
<td>2.29 ± 0.16±A</td>
<td>2.12 ± 0.12±E</td>
</tr>
<tr>
<td></td>
<td>W20</td>
<td>7.27 ± 4.27±A</td>
<td>4.47 ± 0.18±A</td>
<td>2.32 ± 0.16±A</td>
<td>1.93 ± 0.11±E</td>
</tr>
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</table>

Stomatal conductance under different soil water status: The gs 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, gs of M. dianthera in the morning was larger than in the afternoon at all water statuses. The responses of gs of the two species to soil water were similar to that of PNmean. That is, gs in W90 was higher than in W20 both in the morning and in the afternoon. There was no significant difference for M. hangchowensis at W90, W60, or W40, while for M. dianthera, W60 and W40 were higher than W90 and W20 in the morning and afternoon. Compared with M. dianthera, gs values of M. hangchowensis were lower at all water treatments, and the largest and the smallest difference occurred at W20 and W90, respectively. The two species showed a similar pattern in which PN increased gradually with gs in W90 (Fig. 3). However, PN of M. hangchowensis was enhanced more obviously by a slight increase of gs than that of M. dianthera, which suggested that PN of M. hangchowensis was more sensitive to gs 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_{60}, W_{90}, W_{40}, W_{20}, respectively.

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_{60} and W_{20}/W_{40} (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 $P_{N\text{mean}}$, 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. 1997).
There were obvious physiological plasticities in *M. hangchowensis* and *M. dianthera* response to soil water status. Both species had the highest $P_{\text{N mean}}$, $g_s$, 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 $P_{\text{N mean}}$ 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*.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>M. hangchowensis</th>
<th>M. dianthera</th>
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</thead>
<tbody>
<tr>
<td>$P_{\text{N mean}}$ [µmol(CO$_2$) m$^{-2}$ s$^{-1}$]</td>
<td>0.56</td>
<td>0.44</td>
</tr>
<tr>
<td>$g_s$ (a.m.) [mol m$^{-2}$ s$^{-1}$]</td>
<td>0.79</td>
<td>0.48</td>
</tr>
<tr>
<td>$g_s$ (p.m.) [mol m$^{-2}$ s$^{-1}$]</td>
<td>0.63</td>
<td>0.50</td>
</tr>
<tr>
<td>WUE [mmol mol$^{-1}$]</td>
<td>0.41</td>
<td>0.38</td>
</tr>
<tr>
<td>Chl $a$ [g kg$^{-1}$(DM)]</td>
<td>0.24</td>
<td>0.16</td>
</tr>
<tr>
<td>Chl $b$ [g kg$^{-1}$(DM)]</td>
<td>0.14</td>
<td>0.07</td>
</tr>
<tr>
<td>Chl $a/b$</td>
<td>0.23</td>
<td>0.21</td>
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</table>

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.
References