

Effects of light intensity on growth of four *Mosla* species

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Abstract. We compared the growth characteristics of four *Mosla* species that occurred under three light conditions that simulated shaded forest understory, forest edge, and open land. Root mass (M_{root}), stem mass (M_{stem}), leaf mass (M_{leaf}), total mass (M_{total}), root mass ratio (RMR), and root shoot ratio (R/S) all decreased with decreasing light intensity while specific leaf area (SLA), leaf area ratio (LAR), and height ratio (HR) increased as growth light declined. At low light intensity, *M. scabra*, acclimating to a shade environment, had the highest biomass, RMR, R/S, SLA, and LAR, but its plasticity in response to light intensity was lower than that of the other three shade-intolerant species. The results supported the hypothesis that shade-intolerant species have greater plasticity than shade-tolerant species. Compared with *M. scabra* and *M. dianthera*, *M. hangchowensis* and *M. chinensis* had lower competitive ability for water, nutrients and light (indicated by lower RMR, R/S and HR values), which could cause their endangerment and rarity, respectively.

Keywords: Endangerment; Growth; Light intensity; *Mosla chinensis*; *M. dianthera*; *M. hangchowensis*; *M. scabra*; Plasticity; Rarity.

INTRODUCTION

Light is one of the most important environmental factors affecting plant survival, growth, reproduction, and distribution. First, light intensity affects photosynthesis, and this, in turn, is related to the accumulation of organic matter and biomass. Moreover, to sustain higher photosynthetic capacity or survival, plants modify their morphology and biomass allocation at different light conditions (Sims and Pearoy, 1992; Den Dubblede and Oosterbeek, 1995; Feng et al., 2004). For example, plants grown at low light intensities have higher specific leaf areas (SLA) and leaf area ratios (LAR), and lower biomasses and root shoot ratios (R/S) (Semb, 1996; Lentz and Cipollini, 1998; Kremer and Kropff, 1999). Different species, however, respond differently to light intensity. Light-demanding species are more flexible in both morphology and biomass allocation in response to light change than shade-tolerant species (Lortie and Aarssen, 1996; Valladares et al., 2000). Ryser and Eek (2000) suggested the adaptive phenotypic plasticity differences among species may contribute to their different abilities to occupy variable and diverse habitats in the nature. Thus, studies on the plasticity responses of plants, especially endangered and

rare species, to light environments will contribute to our understanding of the ecological mechanism of plant distribution and assist in the development of conservation approaches to endangered and rare species.

Mosla is an annual herb in the family Labiatae. As an endemic plant in China, *M. hangchowensis* only has several small local populations, which were found along the coast in China's subtropical zone. It has become endangered because the number and size of its distribution areas are decreasing quickly due to recent human activities (Chang et al., 1999; Ge and Chang, 2001). *Mosla chinensis* is distributed in the southern Yangtze River drainage area in China, and it is usually the concomitant species in a community because it has just a few individuals in each population (Guan et al., 2003, 2004). In contrast, *M. dianthera* and *M. scabra* are widely distributed in most parts of the subtropical and tropical zones in China and in other countries in East and Southeast Asia, where they are often dominant in their communities (Fang et al., 1989). In the field ecology studies, we found that the habitats of the four species were open land, forest edge, and forest understory. But *M. hangchowensis*, *M. dianthera* and *M. chinensis* are mainly distributed in open land or forest edge with ample sunlight while *M. scabra* is often found in shaded and moist conditions, such as the forest understory (Zhang and Xu, 1988). In this study, we grew the four *Mosla* species under three light intensities. The objectives were to com-

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pare the effects of light intensity on the plants' biomass, biomass allocation, and morphological characters, to analyze the relative importance of these characters in response to light intensity, and to find reasons for the endangerment of *M. hangchowensis* and the rarity of *M. chinensis*.

MATERIALS AND METHODS

Plants and treatments

The research was conducted at the plantation of Zhejiang University, Hangzhou, Southeast China (120°10' E, 30°15'N). Four *Mosla* species were grown in 17 × 15 cm (depth × diameter) pots (three plants per pot) with a mixture of field soil and vermiculite (2:1 v/v) at the end of May 2003 until the seeds germinated and the seedlings reached 5 cm. One week later, they were transferred to three different light conditions: high light (full ambient light, approximately 56.2 mol m⁻² day⁻¹), medium light (about 70% full ambient light, 39.3 mol m⁻² day⁻¹), and low light (25% full ambient light, 14.0 mol m⁻² day⁻¹). The light was controlled by different layers of nylon-net shade (placed 2 m above ground) to simulate the light conditions of open land, forest edge, and forest understory, respectively. The seedlings were irrigated at regular periods depending on the weather and soil moisture status. Each treatment was performed thrice.

Measurements and calculation

At the vigorous vegetation growth period of the four species (mid-July), six individuals of each treatment and species were harvested from the three replication's pots. The height of the individuals was measured before harvest. Leaf area (LA) 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 mass per unit of total mass (leaf mass ratio, LMR), branch mass per unit of total mass (branch mass ratio, BMR), root mass per unit of total mass (root mass ratio, RMR), root mass/shoot mass (root shoot ratio, R/S), leaf area per unit leaf mass (specific leaf area, SLA), leaf area per unit of total mass (leaf area ratio, LAR), and height per unit of total mass (height ratio, HR) were calculated according to Hunt (1978) and Sakai (1995).

Statistical analysis

Statistical analysis was conducted using SPSS 13.0 for Windows (SPSS Inc., Chicago, USA). Differences of the twelve parameters—root mass (M_{root}), stem mass (M_{stem}), leaf mass (M_{leaf}), total mass (M_{total}), LMR, BMR, RMR, R/S, LA, SLA, LAR and HR—among species, light treatments, and interactions were tested by two-way ANOVA. When species effects were significant, significant differences between species in the same treatment and those between treatments in the same species were tested by Duncan's multiple range test. When species × light interactions were significant, plasticity index was calculated for each significant variable and spe-

cies according to Valladares et al. (2000), by dividing the difference between the minimum and the maximum mean values among the three light treatments by the maximum mean value.

Hierarchical cluster analysis was used to determine the relative similarity between the four species or between species clusters based on above twelve parameters. Cluster amalgamation was done with the single linkage method, and the results were plotted as a dendrogram.

RESULTS

Biomass

There were no significant species × light interactions in M_{root} , M_{stem} , M_{leaf} and M_{total} , but they tended to decrease with decreased growth light intensity (Tables 1-2). *Mosla scabra* had the highest M_{root} , M_{stem} , M_{leaf} and M_{total} under low light conditions, but the differences from the other three species were insignificant at high light. M_{stem} , M_{leaf} and M_{total} did not differ among *M. hangchowensis*, *M. chinensis* and *M. dianthera* at the same light intensity, but for M_{root} , *M. dianthera* was higher than both *M. hangchowensis* and *M. chinensis* under medium light conditions (Table 2).

Biomass allocation

There were no significant differences between species and interactions in LMR and BMR (Table 1). RMR and R/S of four *Mosla* species decreased with decreasing light intensity (Figure 1). Under low light conditions, RMR

Table 1. Two-way ANOVA of biomass, biomass allocation, and morphological characters parameters of four *Mosla* species grown at three light conditions.

| Parameters | Species | Light | Species × Light |
|--|--------------|--------------|-----------------|
| M_{root} (g) | 0.004 | 0.000 | 0.128 |
| M_{stem} (g) | 0.010 | 0.000 | 0.063 |
| M_{leaf} (g) | 0.000 | 0.000 | 0.602 |
| M_{total} (g) | 0.002 | 0.000 | 0.279 |
| LMR (g g ⁻¹) | 0.276 | 0.034 | 0.971 |
| BMR (g g ⁻¹) | 0.759 | 0.000 | 0.536 |
| RMR (g g ⁻¹) | 0.019 | 0.000 | 0.013 |
| R/S | 0.002 | 0.000 | 0.001 |
| LA (cm ²) | 0.000 | 0.000 | 0.037 |
| SLA (cm ² g ⁻¹) | 0.000 | 0.000 | 0.028 |
| LAR (cm ² g ⁻¹) | 0.000 | 0.000 | 0.144 |
| HR (cm g ⁻¹) | 0.000 | 0.000 | 0.000 |

M_{root} , M_{stem} , M_{leaf} , M_{total} : the mass of root, stem, leaf, and total, respectively; LMR: Leaf mass ratio; BMR: branch mass ratio; RMR: root mass ratio; R/S: root shoot ratio; LA: leaf area; SLA: specific leaf area; LAR: leaf area ratio; HR: height ratio. The bold P-values are statistically significant at P < 0.05.

Table 2. Comparison of the root mass (M_{root}), stem mass (M_{stem}), leaf mass (M_{leaf}), and total mass (M_{total}) of four *Mosla* species grown under high (full ambient light), medium (about 70% full ambient light), and low (about 25% full ambient light) light conditions.

| Biomass parameters | Light intensities | Species | | | |
|------------------------|-------------------|--------------------------|-------------------------|--------------------------|-------------------------|
| | | <i>M. hangchowensis</i> | <i>M. chinensis</i> | <i>M. dianthera</i> | <i>M. scabra</i> |
| M_{root} (g) | High | 0.75±0.09 ^{aA} | 0.79±0.21 ^{aA} | 0.89±0.22 ^{aA} | 0.88±0.25 ^{aA} |
| | Medium | 0.59±0.20 ^{aAB} | 0.47±0.09 ^{bB} | 0.64±0.12 ^{bA} | 0.60±0.05 ^{bA} |
| | Low | 0.11±0.06 ^{bB} | 0.11±0.04 ^{cB} | 0.12±0.08 ^{cB} | 0.31±0.05 ^{cA} |
| M_{stem} (g) | High | 1.08±0.24 ^{aA} | 1.07±0.17 ^{aA} | 1.18±0.16 ^{aA} | 1.07±0.12 ^{aA} |
| | Medium | 1.08±0.20 ^{aAB} | 0.92±0.21 ^{aB} | 0.93±0.29 ^{aB} | 1.24±0.21 ^{aA} |
| | Low | 0.50±0.17 ^{bB} | 0.49±0.11 ^{bB} | 0.53±0.25 ^{bAB} | 0.75±0.24 ^{bA} |
| M_{leaf} (g) | High | 1.22±0.28 ^{aA} | 1.10±0.12 ^{aA} | 1.09±0.15 ^{aA} | 1.23±0.18 ^{aA} |
| | Medium | 1.19±0.13 ^{aAB} | 1.02±0.24 ^{aB} | 1.02±0.14 ^{aB} | 1.24±0.23 ^{aA} |
| | Low | 0.51±0.18 ^{bB} | 0.46±0.19 ^{bB} | 0.44±0.15 ^{bB} | 0.75±0.18 ^{bA} |
| M_{total} (g) | High | 3.05±0.60 ^{aA} | 2.96±0.49 ^{aA} | 3.15±0.48 ^{aA} | 3.18±0.52 ^{aA} |
| | Medium | 2.86±0.51 ^{aAB} | 2.40±0.52 ^{aB} | 2.59±0.45 ^{aAB} | 3.08±0.49 ^{aA} |
| | Low | 1.12±0.40 ^{bB} | 1.05±0.33 ^{bB} | 1.10±0.33 ^{bB} | 1.81±0.48 ^{bA} |

The data are the means ± SD (n = 6). Different small letters indicate significant differences among three light conditions of the same species ($P < 0.05$). Different capital letters indicate significant differences among four species under the same light conditions ($P < 0.05$).

and R/S of *M. scabra* were significantly higher than the other three species. At high and medium light conditions, however, *M. dianthera* had the highest RMR and R/S (Figure 1).

Morphological characters

LA of the four species was the largest under medium light conditions. For *M. hangchowensis*, *M. dianthera* and *M. chinensis*, LA was significantly larger at high light than that at low light. In *M. scabra*, however, no difference in LA between high and low light emerged (Table 3). SLA

and LAR of the four species increased with decreasing light intensity. Under medium light conditions, SLA and LAR showed no significant differences among four species. Under high and low light conditions, however, *M. scabra* had the highest SLA and LAR, followed by *M. hangchowensis*, and the lowest for *M. chinensis* and *M. dianthera* (Table 3). HR of the four species also increased with decreasing light intensity. Under the same light conditions, *M. dianthera* had the highest HR, but there were no significant differences among other three species (Table 3).

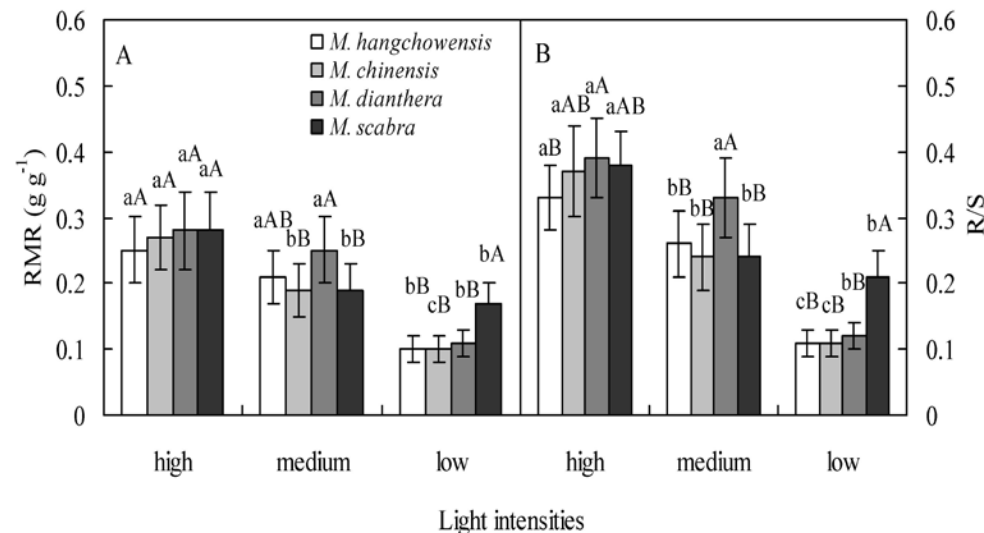


Figure 1. Comparison of root mass ratio (RMR; A), root shoot ratio (R/S; B) of four *Mosla* species grown under high (full ambient light), medium (about 70% full ambient light), and low (about 25% full ambient light) light conditions. The data are the means ± SD (n = 6). Different small letters in each graph indicate significant differences among three light conditions of the same species ($P < 0.05$). Different capital letters in each graph indicate significant differences among four species under the same light conditions ($P < 0.05$).

Table 3. Comparison of leaf area (LA), specific leaf area (SLA), leaf area ratio (LAR) and height ratio (HR) of four *Mosla* species grown under high (full ambient light), medium (about 70% full ambient light), and low (about 25% full ambient light) light conditions.

| Morphological characters | Light intensities | Species | | | |
|--|-------------------|----------------------------|-----------------------------|----------------------------|----------------------------|
| | | <i>M. hangchowensis</i> | <i>M. chinensis</i> | <i>M. dianthera</i> | <i>M. scabra</i> |
| LA (cm ²) | High | 151.03±20.81 ^{bB} | 113.34±20.19 ^{bC} | 109.28±16.78 ^{bC} | 173.62±21.93 ^{bA} |
| | Medium | 228.25±26.78 ^{aA} | 191.34±24.64 ^{aB} | 188.57±25.24 ^{aB} | 247.35±26.74 ^{aA} |
| | Low | 108.11±19.66 ^{cB} | 88.11±19.15 ^{cB} | 85.07±20.43 ^{cB} | 179.19±25.36 ^{cA} |
| SLA (cm ² g ⁻¹) | High | 123.80±13.80 ^{bB} | 103.25±14.70 ^{bC} | 100.57±13.56 ^{bC} | 141.72±14.00 ^{cA} |
| | Medium | 191.81±17.33 ^{aA} | 188.15±13.86 ^{aA} | 184.78±14.60 ^{aA} | 199.48±21.50 ^{bA} |
| | Low | 211.98±18.70 ^{aB} | 192.92±15.68 ^{aBC} | 191.34±12.78 ^{aC} | 240.18±17.13 ^{aA} |
| LAR (cm ² g ⁻¹) | High | 49.52±6.14 ^{bA} | 38.28±4.96 ^{bB} | 34.69±4.96 ^{bB} | 54.60±7.25 ^{cA} |
| | Medium | 79.81±8.57 ^{aA} | 79.63±9.96 ^{aA} | 72.75±8.22 ^{aA} | 80.31±13.12 ^{bA} |
| | Low | 96.53±16.4 ^{aAB} | 83.68±8.80 ^{aBC} | 77.48±9.96 ^{aC} | 99.00±13.78 ^{aA} |
| HR (cm g ⁻¹) | High | 11.28±3.10 ^{bB} | 13.44±2.29 ^{bB} | 21.59±3.85 ^{cA} | 12.97±2.21 ^{bB} |
| | Medium | 14.43±2.53 ^{bB} | 15.56±2.65 ^{bB} | 35.57±4.80 ^{bA} | 15.00±2.55 ^{bB} |
| | Low | 23.07±4.16 ^{aB} | 27.73±4.71 ^{aB} | 47.22±4.97 ^{aA} | 25.66±4.36 ^{aB} |

The data are the means ± SD (n = 6). Different small letters indicate significant differences among three light conditions of the same species ($P < 0.05$). Different capital letters indicate significant differences among four species under the same light conditions ($P < 0.05$).

Plasticity index

There were significant interactions of species × light in RMR, R/S, LA, SLA and HR (Table 1). For most of the five parameters, *M. dianthera* had the greatest phenotypic plasticity, followed by *M. chinensis* and *M. hangchowensis*, with *M. scabra* being the lowest (Table 4). The same trend was found in the mean plasticity index, but the mean plasticity index of *M. scabra* was significantly lower than for other three species, and *M. dianthera*, *M. hangchowensis* and *M. chinensis* exhibited no significant differences.

DISCUSSION

Phenotypic plasticity is the environmental modification of genotypic expression and an important means by which individual plants respond to changing environment (Macdonald et al., 1988). In the present study, light intensity strongly affected the biomass, biomass allocation,

and morphological characters of the four *Mosla* species (Table 1). M_{root} , M_{stem} , M_{leaf} , M_{total} , RMR and R/S decreased with decreasing light intensity while SLA, LAR, and HR increased as growth light declined. These latter are very plastic growth traits and strongly affected by light availability (Jeangros and Nösberger, 1992; Sakai, 1995; Pothier and Prévost, 2002). Decreasing light intensities caused an increase in LAR with the result that light captured by the leaves increased (Semb, 1996). SLA may reflect the leaf thickness to some extent (Augspurger, 1984; Jones and Mcleod, 1990), and it is the most important component affecting LAR (Kremer and Kropff, 1999). Generally, an increase in SLA with decreasing light intensity might compensate for the reduced photosynthesis per unit leaf area and cause overall photosynthesis per plant to be equal (Kremer and Kropff, 1999). Significantly lower photosynthesis at low light intensity was found in the four *Mosla* species in our previous study (Liao et al.,

Table 4. Plasticity indices for root mass ratio (RMR), root shoot ratio (R/S), leaf area (LA), specific leaf area (SLA), and height ratio (HR) in four *Mosla* species.

| Parameters | <i>M. hangchowensis</i> | <i>M. chinensis</i> | <i>M. dianthera</i> | <i>M. scabra</i> |
|--|-------------------------|------------------------|------------------------|------------------------|
| RMR (g g ⁻¹) | 0.60 | 0.61 | 0.62 | 0.38 |
| R/S | 0.67 | 0.69 | 0.69 | 0.46 |
| LA (cm ²) | 0.53 | 0.54 | 0.55 | 0.30 |
| SLA (cm ² g ⁻¹) | 0.42 | 0.46 | 0.47 | 0.41 |
| HR (cm g ⁻¹) | 0.51 | 0.52 | 0.54 | 0.49 |
| Mean ± SD | 0.54±0.09 ^a | 0.56±0.09 ^a | 0.58±0.08 ^a | 0.41±0.08 ^b |

Different letters indicate significant differences ($P < 0.05$).

2005). In this study, therefore, higher SLA and LAR under low light conditions could be parts of the strategy the four *Mosla* species use to acclimate to the shade environment, but lower M_{root} , RMR, and R/S would reduce nutrient and water absorption capacity.

Under 25% full ambient light conditions, *M. scabra* had higher biomass, RMR, R/S, SLA and LAR than the other three species. This was consistent with the shade and moist in the natural habitat of *M. scabra*, as well as the ample sunlight conditions for the other three species. In the three shade-intolerant species, the endangered *M. hangchowensis* and rare *M. chinensis* had M_{stem} , M_{leaf} and M_{total} similar to *M. dianthera* at the same light intensity, but their lower M_{root} , RMR and R/S under full and 70% full ambient light conditions might be the cause of their lower competitiveness for water and nutrients in their favorable habitats than *M. dianthera*. Moreover, the significantly lower HR indicated the competitiveness for light of *M. hangchowensis* and *M. chinensis* was lower than *M. dianthera* because higher HR means more competition for light when total mass is similar (Sakai, 1995; Pothier and Prévost, 2002).

In general, significant species \times light interaction indicates that species respond differently to growth light (González and Gianoli, 2004). In this study, significant interactions in RMR, R/S, LA, SLA and HR were found, and their plasticity indices were lower in *M. scabra* than in the other three *Mosla* species. This is consistent with the hypothesis that shade-tolerant species have lower plasticity than shade-intolerant species (Lortie and Aarssen, 1996; Valladares et al., 2000). Moreover, the highest values of biomass, RMR, R/S, SLA and LAR in a low light environment caused *M. scabra* to separate from the

other three species at 25% ambient light intensity (Figure 2C). For the other three shade-intolerant species, *M. hangchowensis* and *M. chinensis* were separated from *M. dianthera* under full ambient light and 70% ambient light, their favorite light intensities (Figures 2A and B). This was because *M. hangchowensis* and *M. chinensis* had lower M_{root} , RMR, R/S and HR and thus had lower competitive ability for water, nutrients, and light, which may have reduced their abilities to extend their populations, hence causing them to be endangered and rare, respectively.

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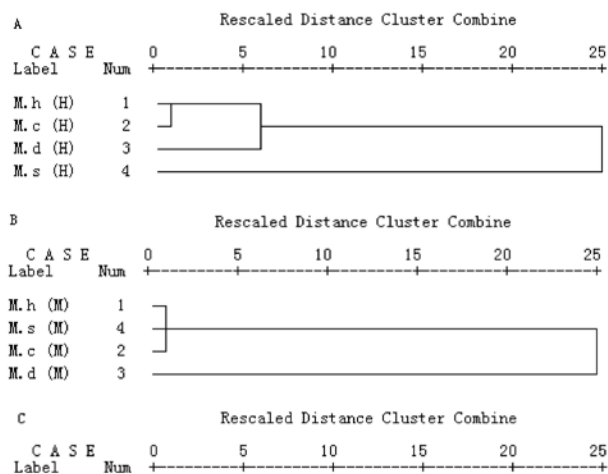


Figure 2. Dendrogram of hierarchical cluster analysis of four *Mosla* species based on 12 parameters at high (full ambient light, A), medium (about 70% ambient light, B) and low (about 25% ambient light, C) light conditions. M.c, *M. chinensis*; M.d, *M. dianthera*; M.h, *M. hangchowensis*; M.s, *M. scabra*. H, M, L in parentheses indicates high, medium, and low light conditions, respectively.

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石薺苧屬 (*Mosla*) 四種植物生長特徵對光強回應

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石薺苧屬 (*Mosla*) 四種植物在三種光強 (100%, 70%, 25% 自然光) 下生長, 其根、莖、葉生物量和總生物量、根生物量比 (RMR) 和根冠比 (R/S) 均隨光強的降低而降低, 比葉面積 (SLA)、葉面積比率 (LAR) 和株高比 (HR) 則隨光強的降低而增加。在低光下, 適生於陰生環境的石薺苧 (*M. scabra*) 具有最大的生物量、RMR、R/S、SLA 和 LAR, 但是它對光強反應的可塑性低於其他三個非陰生物種。與相同光強下的石薺苧和小魚仙草 (*M. dianthera*) 相比, 杭州石薺苧 (*M. hangchowensis*) 和華薺苧 (*M. chinensis*) 具有更低 RMR、R/S 和 HR, 這些有可能使它們對水、營養和光的競爭能力弱, 從而導致了它們分別瀕危和稀少。

關鍵詞: 瀕危; 生長特徵; 光強; 華薺苧; 小魚仙草; 杭州石薺苧; 石薺苧; 可塑性; 稀少。