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Plasticity in photosynthesis and functional leaf traits of *Meconopsis horridula* var. *racemosa* in response to growth irradiance

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ABSTRACT. *Meconopsis horridula* var. *racemosa*, a valuable horticultural and medicinal plant, grows in the high mountains of the Himalayas under a range of light intensities, from bright illumination on the screes to low light in the understory of shrubs. To understand how this species adapts to these various environments, we examined the relative significance of leaf traits and physiology on photosynthetic light acclimation. Compared with plants exposed to low growth irradiance, those under greater irradiance exhibited a higher photosynthetic rate, leaf nitrogen content per unit area (N_a), leaf dry mass per unit area (LMA), chlorophyll a/b ratio and CO_2 diffusion conductance. However, photosynthetic nitrogen-use efficiency and leaf N content per unit mass remained relatively constant regardless of light regime. This change in photosynthetic rate under different light conditions was linked to N_a, LMA and CO_2 diffusion conductance. Our results show that *M. horridula* has high photosynthetic plasticity in response to growth irradiance, and that photosynthetic performance is better from plants grown under brighter illumination. Such findings will be beneficial when developing a cultivation strategy in commercial production.

Keywords: Chlorophyll fluorescence; Growth irradiance; Leaf mass per unit area; Leaf nitrogen; Photosynthesis.

Abbreviations: ***A*,** photosynthetic rate (μmol $m^{-2}s^{-1}$); A_{max}, light-saturated photosynthetic rate (μmol $m^{-2}s^{-1}$); **Chl,** chlorophyll content (mg dm^{-2}); **ETR,** apparent rate of photosynthetic electron transport in PSII (μmol $m^{-2}s^{-1}$); F_v/F_m, maximum photochemical efficiency of PSII; F_v'/F_m', efficiency of excitation energy capture by open reaction centers; g_m, mesophyll conductance (mol $m^{-2}s^{-1}$); g_s, stomatal conductance (mol $m^{-2}s^{-1}$); **HL,** high light; **IL,** intermediate light; J_{max}, light saturated rate of electron transport (μmol $m^{-2}s^{-1}$); **LL,** low light; **LMA,** leaf dry mass per unit area (g m^{-2}); N_a, nitrogen content per unit area (g m^{-2}); N_m, nitrogen content per unit mass (g kg^{-1}); ***NPQ*,** non-photochemical quenching; **PNUE,** photosynthetic nitrogen-use efficiency; **PPFD,** photosynthetic photon flux density (μmol $m^{-2}s^{-1}$); **qP,** photochemical quenching coefficient; V_{cmax}, maximum RuBP saturated rate of carboxylation (μmol $m^{-2}s^{-1}$); **φPSII,** quantum yield of PSII.

INTRODUCTION

Meconopsis horridula var. *racemosa* (Maxim.) Prain, a well-known horticultural plant with large, blue flowers, has attracted the attention of horticulturalists. This species is also used in China as a traditional herbal medicine because of its anti-inflammatory and analgesic activities (Wang et al., 2003). In its natural habitats of southwest China (alt. 3,000-4,900 m), plants can grow under either high light on the screes or when exposed to low illumination associated with the shrub understory. In the former environment, plants have higher rates of flowering and fruitset, larger flowers and thicker leaves. Although irradiance obviously play an important role in modulating the growth and reproduction of this species, little is known about how these plants adapt to such a wide range of light conditions (Zhang and Hu, 2008).

Acclimation to a light environment is particularly important because photosynthesis is closely related to the production of dry mass (Poorter, 1999; Aleric and Kirkman, 2005). Excess light energy under high-irradiance

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condition can lead to the increased formation of damaging reactive oxygen species as byproducts of photosynthesis, thereby reducing photosynthetic carbon gain (Givnish, 1988; Müller et al., 2001; Aleric and Kirkman, 2005). To optimize their growth under various light environments, plants invoke numerous biochemical and developmental responses (Givnish, 1988; Müller et al., 2001; Terashima et al., 2001). Their photosynthetic capacity adjusts to altered irradiances mainly through changes in leaf N content, leaf mass per unit area, stomatal density and relative allocation of N among different pools within the photosynthetic apparatus (Terashima et al., 2001; Pandey et al., 2003; Trouwborst et al., 2011). However, the relative importance of these physiological and anatomical variations within a given plant material during this acclimation period is not well understood (Le Roux et al., 1999).

Because of its popularity, the gene resource of *Meconopsis* has been increasingly threatened due to habitat destruction and intensive harvesting of plants from their natural environments. Large-scale cultivation under controlled conditions is necessary to meet this rising demand in the ornamental trade (Zhang, 2010). Several members of this *Meconopsis* genus have been cultivated for over 100 years in Europe, but that is not an easy task because of scant information about the optimum growing conditions required for commercial production (Still et al., 2003). Although information about its physiology is particularly relevant for the domestication of this wild species, there are limited studies about the optimum growth environment for *M. horridula* (Still et al., 2003; Zhang and Hu, 2008; Zhang, 2010). As one indicator of its physiological tolerance, the photosynthetic response to light has been used as a critical predictor of plant performance in an altered environment (Pandey and Kushwaha, 2005).

We compared the photosynthetic capacity and related leaf traits of *M. horridula* var. *racemosa* under different irradiances when grown in a nursery. Our goals were to determine the mechanism whereby these plants acclimate to changes in irradiance and to evaluate the relative importance of leaf physiology and anatomy to their photosynthetic adaptations.

MATERIALS AND METHODS

Study site and plant materials

The study was performed at the Zhongdian Experimental Station of Alpine Flower in southwestern China (alt. 3260 m). During the growing season in 2007, the mean air temperature and total precipitation were 12.3°C and 430 mm, respectively. The average relative humidity was 78.2% between May and September, based on data collected from 1958 to 2000 (Zhongdian Meteorological Station).

Meconopsis horridula var. *racemosa* (Maxim.) Prain is a perennial herb with branched stems and numerous blue flowers. Each growing season is approximately 125 d long. This species blooms from June to July, and bears fruit from July to September. We collected seeds from the Hong Mountains (alt. 3,900 m) in September 2005 and sowed them in the nursery in March 2006. On 3 May 2007, the resultant plants were transferred to circular pots (20 cm height × 16 cm diameter) containing a 1:1:1 mixture (v:v:v) of field soil, humus soil, and sand. To establish our test conditions of exposure to three different irradiances, we covered the plants with neutral-density shade net (36% transparency) while they were exposed to photosynthetically active radiation under a natural photoperiod (about 14 h in June). On clear days, the light intensity was recorded between 12:00 h and 14:00 h with a LI-COR 1400 data logger (Lincoln, NE, USA). By adjusting the number of layers from our netting, we achieved three treatment levels of mean photosynthetic flux density (PPFD) during our two-hour recording periods: 1) high light (HL), 1987 μmol $m^{-2}s^{-1}$; 2) intermediate light (IL), 715 μmol $m^{-2}s^{-1}$ (≈36% of sunlight); or 3) low light (LL), 259 μmol $m^{-2}s^{-1}$ (≈13% of full sunlight). All seedlings were fertilized monthly with a liquid nutrient solution and irrigated every 2 to 3 d, depending on the weather and soil-moisture status, to avoid water stress.

Photosynthetic measurements

Between 5 and 14 July 2007, photosynthetic gas exchange and chlorophyll fluorescence in relation to light intensity and CO_2 concentration were recorded from fully expanded leaves, using a LI-6400 portable photosynthesis measuring system with a 6400-40 chlorophyll fluorescence chamber (LI-COR, Lincoln, NE, USA). Before measurements were made, the leaves were dark-adapted by clips for >1 h. After the minimum fluorescence (F_o) was determined under a weak modulated light, we exposed the dark-adapted leaves to a 0.8-s saturating light (8000 μmol $m^{-2}s^{-1}$) to obtain the maximum fluorescence (F_m). The leaves were then illuminated by an actinic light (1200 μmol $m^{-2}s^{-1}$) for 15 min. Photosynthetic light (*A*-PPFD) response curves were made by using an automated protocol built into the LI-COR 6400. That program was configured to advance to the next step if the sum of the three coefficients of variation (CO_2, water vapor, and flow rate) was <0.3%, with a minimum wait time of 3 min. Each leaf was equilibrated to initial conditions by waiting at least 15 min before executing the automated protocol. The response curves of three separate leaves from different plants were developed for 13 combinations of light intensities under controlled levels of CO_2 (370 μmol mol^{-1}), flow rate (500 mmol s^{-1}), leaf temperature (20°C) and leaf-to-air vapor pressure deficits (1.0-1.5 kPa).

Curves for the photosynthetic CO_2 response (A-C_i) and *A*-PPFD were determined with the same leaves. After measurements for the latter were completed, those leaves were exposed to 1200 μmol $m^{-2}s^{-1}$ PPFD and 370 μmol mol^{-1} CO_2 for 15 min. We began recording data at 370 μmol mol^{-1} for the photosynthetic rate together with chlorophyll fluorescence versus internal CO_2 concentration response curves, then decreased the concentration gradually to 0

μmol mol^{-1}, returned it to 370 μmol mol^{-1}, and then increased it further. During this period, the leaf temperature, PPFD, and vapor pressure deficit were set to 20°C, 1200 μmol m^{-2}s^{-1}, and 1.0 to 1.5 kPa, respectively.

For our recovery experiment, the sample leaves were dark-adapted at 20°C for 30 min before the minimum and maximum fluorescence yields were calculated. They were then illuminated at 2000 μmol m^{-2}s^{-1} for 30 min. Afterward, the light source was switched off and the samples were allowed to recover in the dark at 20°C. Values for F_o and F_m were recorded after 30 and 60 min of recovery, respectively.

Determination of leaf traits

After the measurements of photosynthesis were taken, the leaves were harvested and their areas were determined with a LI-3000A leaf area meter (LI-COR, Lincoln, NE, USA). Dry mass was obtained after the tissues were dried for 48 h at 80°C. From this, LMA was calculated as the leaf dry mass per unit area (g m^{-2}). The leaf N content was assessed by a Leco FP-428 nitrogen analyzer (Leco Corporation, St. Joseph, MI, USA). Chlorophyll was extracted per the technique of Moran and Porath (1980), and its content analyzed on a UV-2550 spectrophotometer (Shimadzu, Kyoto, Japan) before being calculated according to the equations of Inskeep and Bloom (1985).

Calculation of parameters

A-PPFD curves were fit by a non-rectangular hyperbola. The light-saturated photosynthetic rate (A_{max}) and dark respiration (R_d) were determined by using Photosyn Assistant v1.1 (Dundee Scientific, Dundee, Scotland, UK) according to the method of Prioul and Chartier (1977). The photosynthetic saturation irradiance was defined as the PPFD value at which the photosynthetic rate reached 95% of its maximum (Marschall and Proctor, 2004). Photosynthetic nitrogen-use efficiency (PNUE) was expressed as the ratio of A_{max} to leaf N content per unit area (N_a).

Using *A*-C_i curves, we calculated the maximum carboxylation rate by Rubisco (V_{cmax}) and light-saturated electron transport (J_{max}) with Photosyn Assistant, based on the photosynthetic model of von Caemmerer and Farquhar (1981). Mesophyll diffusion conductance (g_m) from the internal air space to the chloroplasts was estimated according to the method of Harley et al. (1992) as:

$$g_m = \frac{A}{Ci - \dfrac{\Gamma*[ETR + 8\,(A + R_d)]}{ETR - 4(A + R_d)}} \quad (1)$$

where the rate of dark respiration (R_d) was found from the *A*-PPFD response curve, and Γ^* was the hypothetical CO_2 compensation point in the absence of R_d. The value for Γ^* at 20°C was derived from the value at 25°C through the following equation (Bernacchi et al., 2001):

$$\Gamma^* = \Gamma^*_{25} \times \exp^{(c - \Delta Ha/(R\cdot(T+273.15)))} \quad (2)$$

where Γ^*_{25} was the value of Γ^* at 25°C (42.75 μmol mol^{-1}); *c* and *ΔHa* represented a scaling constant of 19.02 and an excitation energy of 37.83 (kJ mol^{-1}), respectively; *R* was the molar gas constant (8.314 kJ K^{-1} mol^{-1}); and T was the leaf temperature (°C) (Bernacchi et al., 2001). Values for g_m were calculated from our measurements of photosynthetic rates at internal CO_2 concentrations of 100 to 300 μmol mol^{-1}, with the average value of g_m being determined for each leaf (Niinemets et al., 2005). The rate of photosynthetic electron transport (ETR) was obtained from chlorophyll fluorescence measurements.

Statistical analysis

Statistical analysis was performed with SPSS 13.0 (SPSS Inc., Chicago, IL, USA). To estimate the differences among light treatments, we tested the data for chlorophyll fluorescence, photosynthesis and leaf traits by using one-way ANOVA and LSD multiple comparison tests. The relationships between photosynthetic parameters and leaf traits were assessed through Pearson regression analysis.

RESULTS

As expected, the photosynthetic rate of *M. horridula* increased with higher PPFDs (Figure 1). The photosynthetic saturation irradiance was 1174 ± 30 μmol m^{-2}s^{-1} for HL plants, 1158 ± 22 μmol m^{-2}s^{-1} for IL plants, and 972 ± 29 μmol m^{-2}s^{-1} for LL plants. The relationships between ETR and PPFD were similar to those between *A* and PPFD. Values for F_v'/F_m', φPSII, and qP decreased with increas-

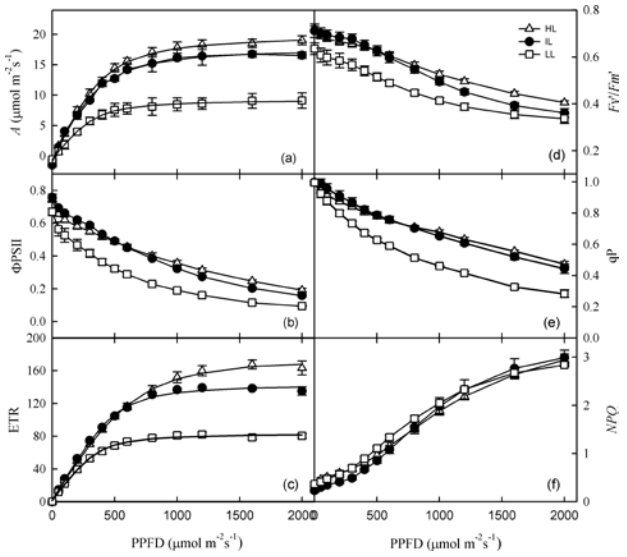

Figure 1. Responses by photosynthetic rate (*A*), quantum yield of PSII (φPSII), electron transport rate of PSII (ETR), efficiency of excitation energy capture by open reaction centers (F_v'/F_m'), photochemical quenching coefficient (qP), and non-photochemical quenching (*NPQ*) to photosynthetic photon flux density (PPFD) in *Meconopsis horridula* grown under different irradiances. Each point represents mean ± 1 SE of 3 measurements from different plants.

ing PPFD, whereas that of *NPQ* was elevated. The HL and IL plants had greater photochemical efficiency (F_v'/F_m', φPSII and qP) compared with LL plants, but values for *NPQ* did not differ significantly regardless of growth irradiances.

Before high light treatments, F_v/F_m was not significantly different among the three growth irradiances ($p > 0.05$; Figure 2). After exposure to 2000 μmol $m^{-2}s^{-1}$ PPFD for 30 min, however, the dark-adapted F_v/F_m values for HL plants decreased by 10.2% from their original readings, while those for IL and LL plants declined by 29.0% and 40.3%, respectively. After 60 min of recovery in the dark, F_v/F_m values were restored to 98.2% (HL), 96.9% (IL) and 89.8% (LL) of the original. The values for F_v/F_m changed in parallel with F_m under the three growth irradiances (Figure 2).

Our A-C_i curves indicated that *M. horridula* had a greater biochemical capacity for photosynthesis under HL compared with LL, and the former plants achieved higher photosynthetic rate at the ambient CO_2 concentration (Figure 3). At C_i concentrations of <400 μmol mol^{-1}, the values for F_v'/F_m' and ETR increased in parallel with rising C_i concentrations, and remained stable or slightly depressed when above that threshold. By contrast, values of *NPQ* exhibited the opposite trend of both F_v'/F_m' and ETR (Figure 3).

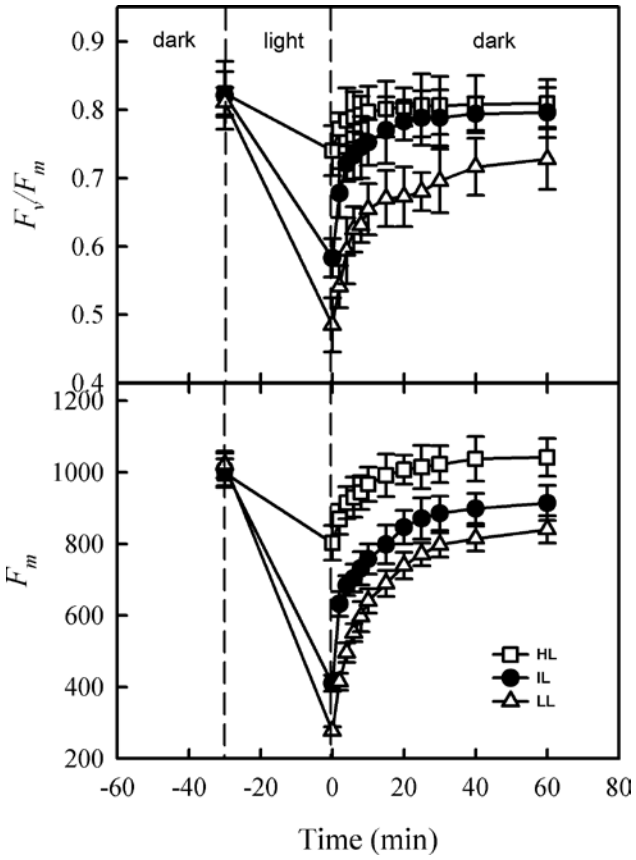

Figure 2. Maximum photochemical efficiency (F_v/F_m) and maximum fluorescence (F_m) of PSII in *Meconopsis horridula* grown under different light intensities. Data were recorded during recovery period that followed 30 min of light-stress treatment at 2000 μmol $m^{-2}s^{-1}$ PPFD. Each point represents mean ± 1 SE of 3 measurements.

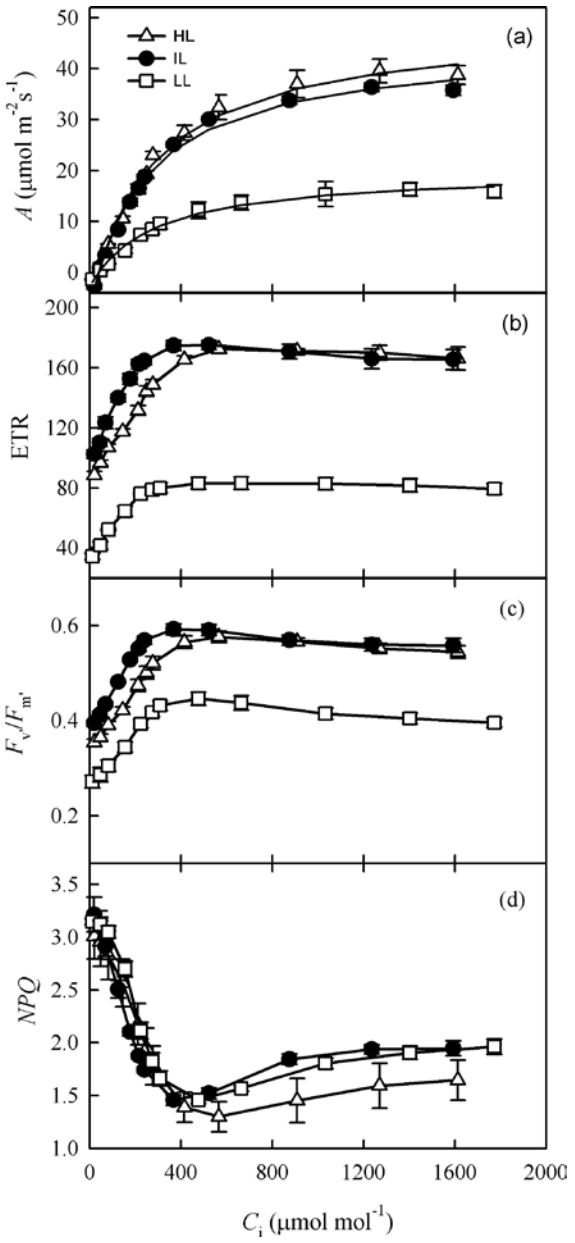

Figure 3. Photosynthetic rate (A), electron transport rate of PSII (ETR), efficiency of excitation energy capture by open reaction centers (F_v'/F_m') and non-photochemical quenching (NPQ) of *M. horridula* in response to intercellular CO_2 concentration. Each data point represents mean ± 1 SE of 3 measurements from different plants.

At saturating irradiances, the photosynthetic rate of HL and IL plants were higher than that of LL plants ($p < 0.001$; Figure 4). Plants exposed to either HL or IL conditions had higher stomatal conductance (g_s) and mesophyll conductance (g_m) than those receiving the LL treatment (Figure 4). A close positive relationship was found between A_{max} and g_s ($r = 0.762$, $p < 0.05$) or g_m ($r = 0.849$, $p < 0.01$) (Figure

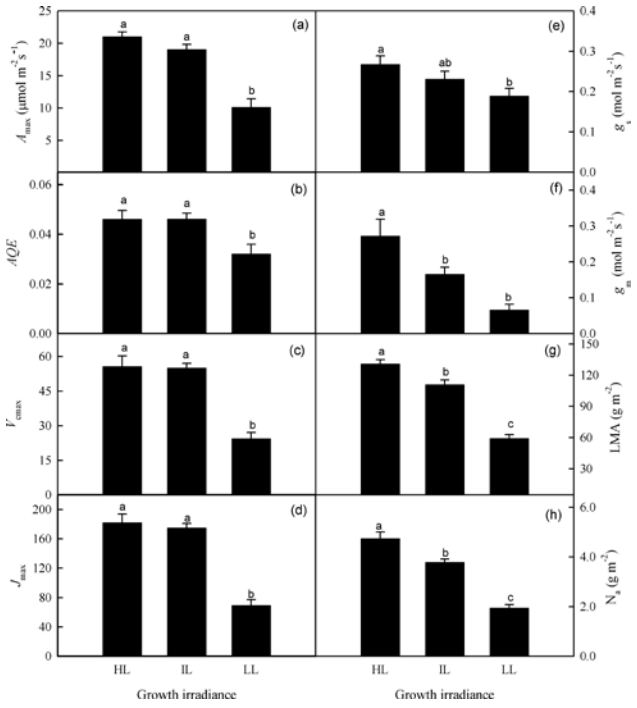

Figure 4. Light-saturated photosynthetic rate (A_{max}), apparent quantum efficiency (AQE), maximum RuBP-saturated rate of carboxylation (V_{cmax}), light-saturated rate of electron transport (J_{max}), stomatal conductance (g_s), mesophyll conductance (g_m), leaf mass per unit area (LMA) and leaf nitrogen content per unit area (N_a) from *Meconopsis horridula* grown under three irradiances. Different letters above bars in each graph indicate statistically different mean values ($p \leq 0.05$), as determined by LSD multiple comparison tests.

5). The LMA increased with growth irradiance (Figure 4), and showed a significantly positive correlation with g_s or g_m (Figure 6). Although no significant difference in N_m was noted regardless of light treatment ($p > 0.05$), values for N_a were higher under HL or IL conditions than under LL because of their larger LMA (Figure 4). The N_a was significantly correlated with LMA, J_{max}, and V_{cmax} (Figure 6). However, PNUE did not different among our light regimes ($p > 0.05$). Chlorophyll contents per unit area were higher under IL than under either HL or LL (Figure 7), but the Chl a/b ratio increased with growth irradiance (Figure 7). However, chlorophyll content was not correlated with A_{max} (Figure 5).

DISCUSSION

Our findings demonstrate that when plants of *M. horridula* are grown in a high-light environment their photosynthetic performances are better than under low light. This species adapts well to high growth irradiance (Figure 1), and the F_v/F_m values in all light environments can rapidly be recovered due to the relaxation of *NPQ* (Figure 2). The reduction in F_v/F_m under high light was mainly caused by a marked decrease in F_m, a response that might be induced by the inactivation of part of the PSII reaction centers (Figure 2). Furthermore, the marked decline in PSII activity in HL leaves results from the critical loss of D1 protein from those reaction centers (Bertamini et al., 2004). This D1 protein is a target of high light-induced damage to the PSII complex, and its turnover is accelerated when irradiance increases (Aro et al., 1993). Plants have several strategies for avoiding the deleterious effects of excess light energy, such as thermal dissipation (Müller et al., 2001). Higher values of *NPQ* reflect a greater degree of dissipation, a process associated with the xanthophyll cycle (Germino and Smith, 2001). Previous studies have shown that, under high light or environmental stress, *NPQ* can be significantly enhanced to protect the photosynthetic apparatus from photoinhibition by enriching xanthophyll cycle pigments (Golding and Johnson, 2003; Ballottari et al., 2007). Here, the rise in *NPQ* that paralleled changes in light intensity, which indicated that non-photochemical quenching contributes to the photo-protection of *M. horridula*.

Although plants grown under high irradiance had lower Chl contents than those exposed to LL conditions, the former had higher Chl a/b ratios (Figure 7). This result is consistent with those previously reported by researchers such as Pandey and Kushwaha (2005). Usually, the electron transport capacity per unit of Chl is greater under

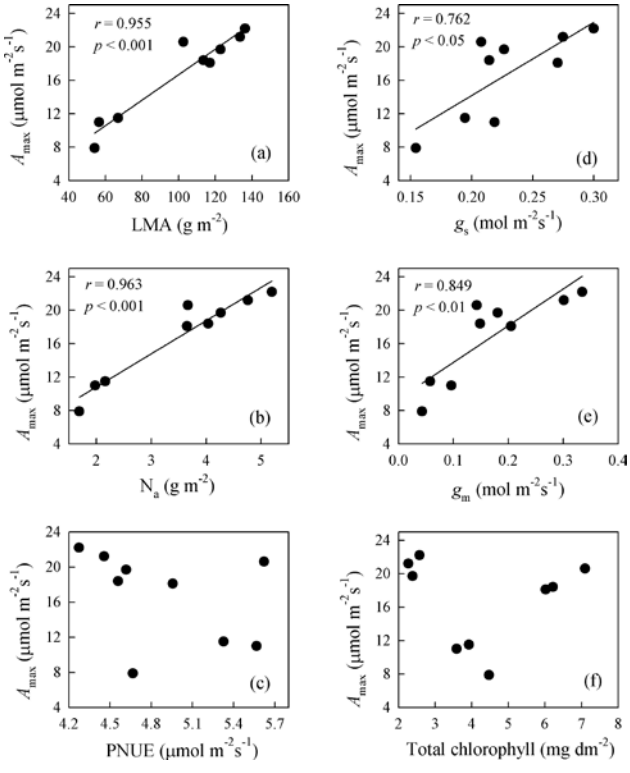

Figure 5. Correlations between light-saturated photosynthetic rate (A_{max}) and leaf dry mass per unit area (LMA), leaf nitrogen content per unit area (N_a), photosynthetic nitrogen-use efficiency (PNUE), stomatal conductance (g_s), mesophyll conductance (g_m) or total chlorophyll content in *Meconopsis horridula*.

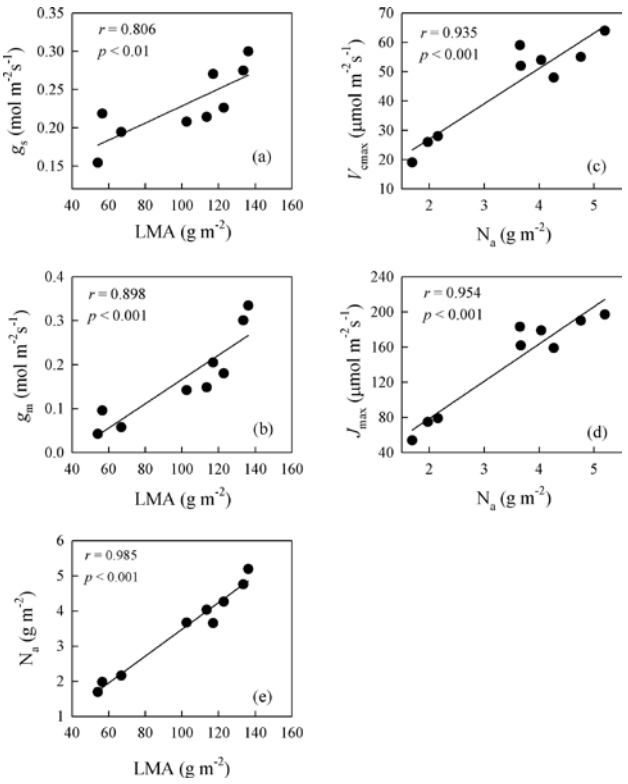

Figure 6. Correlations between leaf dry mass per unit area (LMA) and stomatal conductance (g_s) or mesophyll conductance (g_m); and between leaf nitrogen content per unit area (N_a) and maximum RuBP-saturated rate of carboxylation (V_{cmax}), light-saturated rate of electron transport (J_{max}) or LMA in *Meconopsis horridula*.

high light than at low light due to a relative increase in the amounts of cytochrome *b/f* complex and a coupling factor (Davies et al., 1987). Hikosaka and Terashima (1995) have suggested that the fluctuation in Chl a/b ratios is caused by a change in the ratio of the photosynthetic reaction center to its antenna size. Large antennae are necessary for efficient light capture when light is limiting, but they can be a liability when irradiance is abundant or excessive (Müller et al., 2001). The PSII core complex contains mainly Chl a, whereas LHCII has both Chl a and Chl b. To increase the number of PSII reaction centers for efficient electron transport under high irradiance, the LHCII is reduced, thereby leading to an increased Chl a/b ratio in the leaf (Genty and Harbinson, 1996; Kitajima and Hogan, 2003). Consequently that HL-induced change in this ratio optimizes the nitrogen allocation within a leaf (Hikosaka and Terashima, 1995).

Adjustments to the chlorophyll content and the Chl a/b ratio are apparently integral features in the process of acclimating to contrasting light environments (Kitajima and Hogan, 2003). The reduction in Chl content in HL plants, along with the increase in Chl a/b ratio, was most likely due to changes in the organization of light-harvesting and electron transport components (Schiefthaler et al., 1997). An adjustment in both photosystem stoichiometry and Chl

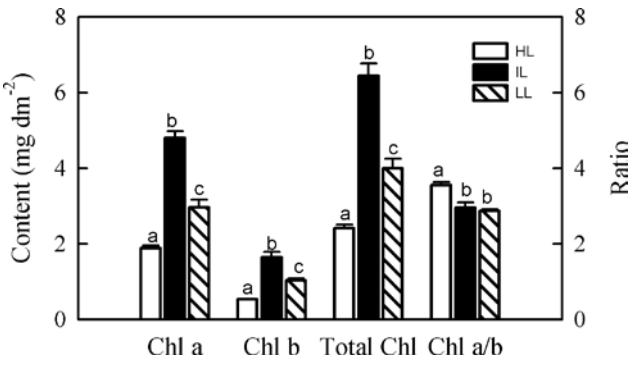

Figure 7. Chlorophyll content per unit area and Chlorophyll a/b ratio from *Meconopsis horridula* leaves grown under three growth irradiances. Different letters above bars for each component indicate statistically different mean values ($p \leq 0.05$), as determined by LSD multiple comparison tests.

a/b ratios can correct the imbalance in light absorption by the two photosystems and can optimize photosynthetic electron transport, thereby minimizing the potential for photo-oxidative damage (Chow et al., 1990; Müller et al., 2001; Kitajima and Hogan, 2003). The Chl a/b ratio in *M. horridula* was significantly lower under LL conditions than under either HL or IL levels, which might suggest that plants exposed to the lower light intensity had a higher ratio of PSII to PSI (Walters and Horton, 1994). Therefore, this alteration could be a compensation strategy to correct for that absorption imbalance, either improving photosynthetic efficiency or decreasing the extent of photo-damage as light levels change.

Meconopsis horridula had a higher light-saturated photosynthetic rate under HL compared with LL. Previous studies have shown that leaf anatomy contributes to this photosynthetic acclimation to growth irradiance (Evans and Poorter, 2001; Terashima et al., 2001; Oguchi et al., 2005). We found that LMA values rose with greater light intensity; such a change in LMA alters the amount of photons that can be intercepted per unit of leaf dry mass (Evans and Poorter, 2001). That is, species with higher LMA accumulate more photon-absorbing compounds in their leaves (Hikosaka, 2004). Previous studies found that leaves exposed to more intense light have a larger area of chloroplasts facing the intercellular space (S_c), which is strongly correlated with A_{max} (Oguchi et al., 2003; Pandey and Kushwaha, 2005). Thicker leaves provide greater open space along the mesophyll cell wall to accommodate additional chloroplasts in order to maximize S_c and, hence, CO_2 assimilation (Terashima et al., 2001; Oguchi et al., 2003). An increase in mesophyll thickness can result in an increase in total S_c per unit leaf area (Terashima et al., 2001). Consequently, leaf thickness determines an upper limit for A_{max} in leaves subjected to a change from low- to high-light conditions (Oguchi et al., 2003). In addition, variation in LMA with growth irradiance can lead to the change of photosynthetic rate and CO_2 diffusion conductance (Zhang et al., 2007). We found a linear relationship

between LMA and g_m, N_a, and A_{max} in *M. horridula* (Figures 5, 6). However, maintaining high photosynthetic capacity is costly to a plant system and is advantageous only under high irradiance because it requires the formation of thick leaves with an accompanying larger investment of nitrogen toward photosynthetic enzymes. In environments with limited light, such an investment would be wasteful (Terashima et al., 2001; Oguchi et al., 2005).

Differences in photosynthesis under different growth irradiances arose partly from biochemical causes, such as because of the large proportion of leaf N present in the photosynthetic apparatus (Evans, 1989); A_{max} is strongly correlated with leaf nitrogen content (Evans, 1989; Hikosaka, 2004). Generally, the leaves on plants grown under low light have more nitrogen content per mass than those exposed to high light (Evans and Poorter, 2001). This is because shade leaves contain less mechanical tissue per unit area than do sun leaves (Niinemets et al., 1998), and also because a greater proportion of N is partitioned into the light-harvesting thylakoid components when light is limiting (Evans, 1989; Frak et al., 2002). Here, N_m values in *M. horridula* were not significantly changed with irradiance, whereas those of N_a increased with growth irradiance. This variability in N_a is essentially caused by shifts in LMA (Frak et al., 2002). We found a close linear relationship between N_a and either V_{cmax} or J_{max} (Figure 6), the latter two could be increased in response to the nitrogen supply (Kitajima and Hogan, 2003). V_{cmax} is related to the content and activity of Rubisco, whereas J_{max} is associated with the regeneration rate of RuBP. Yin and Johnson (2000) showed that light intensity can change the amounts of Rubisco and cytochrome *f*. Moreover, under moderate to high light intensities, the photosynthetic rate is altered by changes in Rubisco activation. This activation is linked to carbamylation of the protein and the removal of inhibitors that block either carbamylation or RuBP-binding to carbamylated sites before reactions with CO_2 or O_2 (Perchorowicz et al., 1981; Brooks et al., 1988; Jensen, 2004).

In conclusion, *M. horridula* plants exhibited a high degree of photosynthetic plasticity in response to different growth irradiances. This was accomplished through modifications to LMA, the Chl a/b ratio and N_a. Photosynthetic performance was better under high irradiance than low irradiance. These results demonstrate that this species prefers more intense light conditions and requires cultivation in an open habitat with adequate sunshine for best growth.

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總狀綠絨蒿光合作用及葉片性狀對生長光強的塑性回應

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總狀綠絨蒿（*Meconopsis horridula* var. *racemosa*）是世界著名的高山花卉和藥用植物。在喜馬拉雅地區，它既能生長於光照強烈的高山流石灘上，也能棲息在低光強的灌木林下。為了瞭解這種植物如何適應不同的光環境，我們研究了葉片性狀和生理在其光適應中的相對作用。與生長在低光強下的植株相比，總狀綠絨蒿在高光強下表現出更高的光合速率、單位面積葉氮含量、比葉重、葉綠素 a/b 比值和 CO_2 擴散導度，但是光合氮利用效率及單位品質的葉氮含量在處理間相對穩定。不同生長光強下光合速率的變化與單位面積的葉氮含量、CO_2 擴散導度和比葉重相關。我們的研究表明總裝綠絨蒿對光強表現高的光合適應塑性，且在高光照下光合表現更好。研究結果對於總裝綠絨蒿栽培策略的制定有重要意義。

關鍵詞：葉綠素螢光；生長光強；比葉重；葉氮；光合作用。