Photosynthetic adaptation of *Meconopsis integrifolia* Franch. and *M. horridula* var. *racemosa* Prain

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ABSTRACT. Both *Meconopsis integrifolia* Franch. and *M. horridula* var. *racemosa* Maxim. are native to the Himalayas and prized as ornamentals and medicinal plants. Cultivating *Meconopsis* is difficult at lower altitudes owing to its intolerance to hot summers. To develop a cultivation strategy and predict plant performance for introduction, we compared the photosynthetic capacity of *M. integrifolia* and *M. horridula* as well as their photosynthetic responses to light and temperature in the nursery at an altitude of 3,260 m. *Meconopsis integrifolia* was more sensitive to high temperature than *M. horridula* while *M. horridula* reached a peak photosynthetic rate at a higher light level than *M. integrifolia*. Compared with *M. integrifolia*, *M. horridula* showed a higher light saturated photosynthetic rate, maximum RuBP saturated rate of carboxylation, light saturated rate of electron transport, stomatal conductance, leaf dry mass, and N content per unit area. The mesophyll conductance and leaf N content per unit mass of the two species were not significantly different. The differences in photosynthetic capacity between two *Meconopsis* species were correlated with their biochemical efficiency and leaf thickness, but not chlorophyll content or mesophyll conductance. The results suggest that, at lower altitudes, introducting and cultivating *M. horridula* could be easier owing to its wider physiological adaptation.

Keywords: Chlorophyll fluorescence; Leaf traits; *Meconopsis*; Photosynthesis; Physiological adaptation.

Abbreviations: **AQE,** apparent CO_2 quantum efficiency (mol CO_2 mol photons^{-1}); **Chl,** chlorophyll content per unit area (mg dm^{-2}); F_v/F_m, potential quantum yield of PSII; **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 (mg g^{-1}); T_{opt}, optimal temperature for photosynthesis; **PPFD,** photosynthetic photon flux density (μmol m^{-2}s^{-1}); **φPSII,** effective quantum yield of PSII; F_v'/F_m', efficiency of excitation energy capture by open reaction centre; **ETR,** apparent rate of electron transport of PSII (μmol m^{-2}s^{-1}); **qP,** photochemical quenching; **NPQ,** non-photochemical quenching; P_N, photosynthetic rate (μmol m^{-2}s^{-1}); P_{Nmax}, light-saturated P_N (μmol m^{-2}s^{-1}); g_m, mesophyll conductance (mol m^{-2}s^{-1}); g_s, stomatal conductance (mol m^{-2}s^{-1}); J_{max}, light saturated rate of electron transport (μmol m^{-2}s^{-1}); V_{cmax}, maximum RuBP saturated rate of carboxylation (μmol m^{-2}s^{-1}).

INTRODUCTION

The majority of the 49 species in the genus *Meconopsis* grow at high elevations (2,135-5,795 m) in the Himalayas and other mountains in western China. Only *M. cambrica* can be found in Europe (Chuang, 1981). As famous horticultural plants bearing large and beautiful flowers, *Meconopsis* have attracted the attention of botanists. Some *Meconopsis* species can be used as traditional herbal medicine, for they possess anti-inflammatory and analgesic activities (Samant et al., 2005). Several members of the genus have been cultivated over 100 years, but cultivating *Meconopsis* is not an easy task because of the poor performance at lower altitude, especially in summer (Ren,

1993; Still et al., 2003). In addition, habitat destruction has increasingly threatened these valuable gene pools, which are now limited to a narrow range of distribution (Sulaiman and Babu, 1996).

Empirical observations suggest that high temperature during the growing season is an important determinant limiting the growth and development of *Meconopsis* (Norton and Qu, 1987; Ren, 1993). However, the adaptation of *Meconopsis* to temperature is significantly different across species (Ren, 1993). Both *M. punicea* and *M. betonicifolia* grown in colder temperatures have a larger dry weight and flower size than those grown in warmer conditions (Still et al., 2003). *Meconopsis integrifolia* can flower in its native habitat even in the snow. This remarkable tolerance for low temperatures would lead to poor adaptation in warm temperatures. The growth and survival of plants can be determined by the

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thermo-tolerance capabilities of photosynthesis because photosynthetic traits govern carbon acquisition (Sharkey, 2000; Kuo-Huang et al., 2007). High temperature has been shown to alter thylakoid membrane structure, decrease Rubisco activity and RuBP regeneration capacity, perturb photosynthetic electron transport, increase dark respiration and photorespiration, and sequentially affect carbon assimilation (Sharkey, 2000; Wise et al., 2004). Photosynthetic apparatuses can be protected against heat damage by dissipating excessive light energy (Hamerlynck and Knapp, 1996). However, the protective mechanisms are not uniform among plant species, and this affects their acclimation to a new environment (Streb et al., 1998).

Because of their dependency on the availability of solar radiation, plants often show various adaptive strategies to maximize photosynthetic efficiency, depending on their light environments (Givnish, 1988). Insufficient light may reduce carbon gain and growth of plant by limiting photosynthesis. Conversely, high light levels may damage photosynthetic apparatuses (Hjelm and Ögren, 2004). From our field observation, *M. integrifolia* under full sunlight grows poorly when compared to nearby *M. horridula*. Intensive light appears to accelerate leaf aging in *M. integrifolia*. Obviously, these two *Meconopsis* species have divergent adaptation to light, but the nature of this adaptation has not been studied.

After transplanting from natural habitat to nursery, plants may be exposed to uncomfortable environments (Zhang et al., 2005). The growth of plant in the altered environment depends on the physiological tolerance and genetic differentiation since almost all dry weight accumulation is the result of photosynthetic carbon fixation (Wu and Campbell, 2006). Photosynthetic responses to light and temperature have been used to predict plant performance and physiological tolerances to environmental conditions and select growth conditions suitable for different species. Chlorophyll fluorescence measurement is used to assess heat-induced alteration of thylakoid membranes and thermal damage to PSII (Hamerlynck and Knapp, 1996). To date, however, only limited studies on the cultivation and photosynthesis of *Meconopsis* have appeared (Ren, 1993; Still et al., 2003).

Our experiment was designed to compare the photosynthetic capacity and related leaf traits of *M. integrifolia* and *M. horridula*, as well as their photosynthetic responses to light, temperature, and CO_2 concentration in the nursery at an altitude of 3,260 m. *Meconopsis integrifolia* (Maxim.) Fr. is a perennial herb found in rocky or grassy places in sparse woods at altitudes of 3,300-5,100 m in western China and Burma. The leaves and stems are covered with dense hairs. Most plants reach about 50 cm in height. Typically, the basal rosette-leaves may grow to 15-32 cm long and up to 5 cm wide while the upper ones are 5-11 cm long and 0.5-1.0 cm wide. This species usually bears 4-5 yellow flowers from May to June, and the fruits mature from June to August. *Meconopsis horridula* var. *racemosa* (Maxim.)

Prain is also a perennial herb and has sharp spines on the leaves and stems. The stem is branched with many blue or purple flowers. This species occurs on rocky slopes at altitudes of 3,000-4,900 m in southwestern China. The flowering period is June to July, and fruit-setting period July to September. The main goals of this study were to determine: (1) how photosynthetic light and temperature responses differ between the two species, and (2) whether *Meconopsis* species differed in their biochemical capacity for photosynthesis.

MATERIALS AND METHODS

The study was conducted in Zhongdian Experimental Station of Alpine Flower at an altitude of 3,260 m (atmospheric pressure = 69 kPa) in southwest China. For May to September (growing period), mean air temperature and precipitation were 12.3 ± 2.1°C (mean ± SD) and 430 ± 55 mm in 2005, respectively. Relative air humidity from May to September averaged 78.2% during the 1958-2000 period (data obtained from Meteorological Station of Zhongdian County).

The seeds of *M. horridula* var. *racemosa* were collected from Hong Mountain in southwestern China at an altitude of 3,900 m in August 2003 while the seeds of *M. integrifolia* came from Big Snow Mountain at an altitude of 4,200 m in September 2003. The seeds of two species were sown in the nursery in March 2004. The seedlings of both species were grown under full sunlight, fertilized monthly with a liquid nutrient solution during the summer, and watered every 2-3 days as needed. The plants typically took 2 years to reach the flowering stage.

Gas exchange and chlorophyll fluorescence in response to different environmental conditions were measured on fully expanded leaves using a portable photosynthesis system (LI-6400, LI-COR, Lincoln, NE, USA) equipped with a fluorescence chamber (LI-6400-40) in June 3-16 (flowering period), 2005. Before measurement, the leaf was adapted to the dark for more than 10 h. After the minimum fluorescence (F_o) was determined by a weak modulated light, a 0.8 s saturating light was used on the dark-adapted leaf to determine the maximum fluorescence (F_m). The leaf was then illuminated by an actinic light of 1200 µmol m^{-2}s^{-1} (10% blue, 90% red) for 15 min. Then the maximum chlorophyll fluorescence in the light (F_m') was determined by applying an 0.8 s saturating light pulse. After the actinic light had been switched off, a far-red light was exerted to determine the minimal level of fluorescence (F_o'). The photosynthetic light response curves (P_N-PPFD) were made using an automated protocol built into LI-6400. The program was configured to advance to the next step if the sum of three coefficients of variation (CO_2, water vapor, and flow rate) was less than 0.3%, with a minimum waiting time of 3 min. Each leaf was equilibrated to initial conditions by waiting at least 15 min before executing the automated protocol. P_N-PPFD curves of three leaves were measured at the light intensities of 2000, 1600, 1200,

1000, 800, 600, 400, 300, 200, 100, 50 and 0 $\mu mol\ m^{-2}s^{-1}$ under controlled levels of CO_2 (350 $\mu Pa\ Pa^{-1}$), flow rate (500 $\mu mol\ s^{-1}$), leaf temperature (20°C), and vapor pressure deficit (1.0-1.5 kPa).

Photosynthetic CO_2 response curves (P_N-C_i) and P_N-PPFD curves were determined with the same leaves. After completion of P_N-PPFD curve measurement, the leaf was induced at 1200 $\mu mol\ m^{-2}s^{-1}$ light intensity and 350 $\mu Pa\ Pa^{-1}$ CO_2 concentration for 15 min. Photosynthetic rates versus CO_2 response curves together with chlorophyll fluorescence were measured at a leaf temperature of 20°C, PPFD of 1200 $\mu mol\ m^{-2}\ s^{-1}$, and vapor pressure deficit of 1.0-1.5 kPa. P_N-C_i response measurements were started at ambient CO_2 concentration, decreased gradually to 0 $\mu Pa\ Pa^{-1}$, returned to ambient CO_2 concentration, and then increased to a higher concentration to ensure that the stomata stayed open throughout the measurement. The photosynthetic rate and chlorophyll fluorescence were measured at different CO_2 concentrations using the automated protocol built into LI-6400.

The temperature responses of photosynthesis and chlorophyll fluorescence were measured between 10 and 35°C at PPFD of 1200 $\mu mol\ m^{-2}s^{-1}$, CO_2 concentration of 350 $\mu Pa\ Pa^{-1}$ and vapor pressure deficit of 1.0-1.5 kPa. Leaf temperature was adjusted to the desired level using the internal heating/cooling system of the analyzer. Each sample was first dark-adapted for 10 h. Thereafter, the weak measuring light beam was switched on to determine the minimum fluorescence yield F_o. Subsequently, the maximum fluorescence yield F_m was determined by applying a 0.8s saturating light pulse. The light source of gas analyzer was then switched on and the sample was illuminated at PPFD of 1200 μmol photons $m^{-2}s^{-1}$. Leaf temperature was adjusted to 10°C until steady-state photosynthesis was achieved. The values of gas exchange and chlorophyll fluorescence were first recorded immediately. In the experiment with gradually increased temperature, leaf temperature was first elevated from 10°C to the next higher selected temperature at a 5°C increment and maintained constant for 10 min. The same procedure was repeated for each of six tested leaf temperatures in the ranges from 10 to 35°C, with the same leaf being used throughout the entire measurement. The optimal temperature for photosynthesis (T_{opt}) was calculated from the polynomial curve fitted to the temperature response data.

For the recovery experiment, the sample leaf was adapted in the dark at 20°C for 30 min before F_o and F_m were measured. After the leaf was illuminated at 2000 $\mu mol\ m^{-2}s^{-1}$ and 20°C for 30 min, the light source was switched off, and the values of F_o and F_m were measured immediately. Then the leaf was recovered in the dark at 20 °C, and the values of F_o and F_m were recorded after 10, 15, 20, 25, 30, 35, 40 and 60 min of recovery, respectively.

P_N-PPFD curves were fitted by a non-rectangular hyperbola. Light saturated photosynthetic rate (P_{Nmax}), dark respiration (R_d) and apparent CO_2 quantum yield (AQE) were determined for each leaf using Photosyn Assistant v.1.1 (Dundee Scientific, Scotland, UK), which follows the method of Prioul and Chartier (1977).

The mesophyll conductance from the sub-stomatal cavity to chloroplasts (g_m) was estimated according to the method of Harley et al. (1992) as,

$$g_m = \frac{P_N}{C_i - \dfrac{\Gamma*[ETR + 8(P_N + R_d)]}{ETR - 4(P_N + R_d)}} \tag{1}$$

Where the rate of respiration (R_d) was calculated from P_N-PPFD curve in the same leaf. $\Gamma*$ was the hypothetical CO_2 compensation point in the absence of R_d. The values of $\Gamma*$ at 20°C was derived from the value at 25°C according to Bernacchi et al. (2001). g_m was calculated from photosynthetic rate at C_i 100-350 $\mu Pa\ Pa^{-1}$, and the average value of g_m was determined for each leaf. Over this C_i range, the values of g_m are stable (Niinemets et al., 2005).

The chloroplast CO_2 concentration (C_c) was calculated from Equation 2 (Bernacchi et al., 2002).

$$C_c = C_i - P_N/g_m \tag{2}$$

Then using chloroplast CO_2 concentration (C_c) instead of intercellular CO_2 concentration (C_i), the maximum carboxylation rate by Rubisco (V_{cmax}) and light-saturated electron transport (J_{max}) were calculated from P_N-C_c response curves using by Photosyn Assistant software based on the photosynthetic model of von Caemmerer and Farquhar (1981). The values of C_c were adjusted according to the atmospheric pressure at study site when the photosynthetic parameters were calculated. As the software allows us to enter the values of the Michaelis-Menten constant for RuBP carboxylation (K_c), RuBP carboxylation (K_o), and Rubisco specificity factor (τ), the values of K_c, K_o and τ derived from the literature of Bernacchi et al. (2001) were used to calculate V_{cmax} and J_{max}.

The chlorophyll fluorescence parameters were calculated as: (1) potential quantum yield of PSII: $F_v/F_m = (F_m - F_o)/F_m$; (2) effective quantum yield of PSII: $\varphi PSII = (F_m' - F_s)/F_m'$; (3) efficiency of excitation energy capture by open reaction centre: $F_v'/F_m' = (F_m' - F_o')/F_m'$; (4) apparent rate of electron transport of PSII: $ETR = 0.5\varphi PSII Q_{abs}$, where 0.5 was a factor assuming an equal distribution of absorbed photons between PSI and PSII for C_3 plants. Q_{abs} was the absorbed light energy that was calculated as PPFD * leaf absorbance, and leaf absorbance was taken as 0.85; (5) photochemical quenching: $qP = (F_m' - F_s)/(F_m' - F_o')$; (6) non-photochemical quenching: $NPQ = (F_m - F_m')/F_m'$.

The leaves from the sampled plants previously used in photosynthetic measurements were harvested. Leaf areas were measured using a leaf area meter (LI-3000A, LI-COR, Lincoln, NE, USA). Dry mass was determined after drying for 48 h at 70°C. Then, leaf N content was analyzed using a LecoFP-428 N analyzer (Leco Corporation, MI, USA). LMA was calculated as leaf dry mass per unit area.

Chlorophyll was extracted using the technique of Moran and Porath (1980). Chlorophyll content was analyzed with a spectrophotometer (UV-2550, Shimadzu, Japan) and calculated using equations developed by Inskeep and Bloom (1985).

Statistical analysis was performed using SPSS 12.0 (SPSS Inc., Chicago, USA). The differences in photosynthetic parameter and leaf trait among species were tested using an independent t-test. The relationships between photosynthetic parameters and leaf traits were assessed using linear regression analysis.

RESULTS

Photosynthetic rate increased with increasing PPFD (Figure 1). The maximum photosynthetic rate was obtained at PPFD of 1040 μmol $m^{-2}s^{-1}$ for *M. integrifolia* and 1350 μmol $m^{-2}s^{-1}$ for *M. horridula*. The photosynthetic light saturation level of *M. integrifolia* was lower than that of *M. horridula* (*t*=5.063, *p*=0.007). This could be confirmed by chlorophyll fluorescence. For both species, the values of F_v'/F_m', φPSII and qP decreased with increasing PPFD. At low irradiance, the values of qP, φPSII and ETR differed little, but above 400 μmol $m^{-2}s^{-1}$ the values for *M. horridula* were higher than those of *M. integrifolia*. The electron transport rate of *M. integrifolia* reached the maximal at 800 μmol $m^{-2}s^{-1}$ PPFD, with *M. horridula* at 1600 μmol $m^{-2}s^{-1}$ PPFD. From 0 to 2000 μmol m^{-2} s^{-1}, the NPQ of *M. horridula* increased at nearly all times while the NPQ of *M. integrifolia* did not increase above the PPFD of 1200 μmol $m^{-2}s^{-1}$.

Dark acclimated value of F_v/F_m reflects the potential quantum efficiency of PSII and can be used as a sensitive indicator o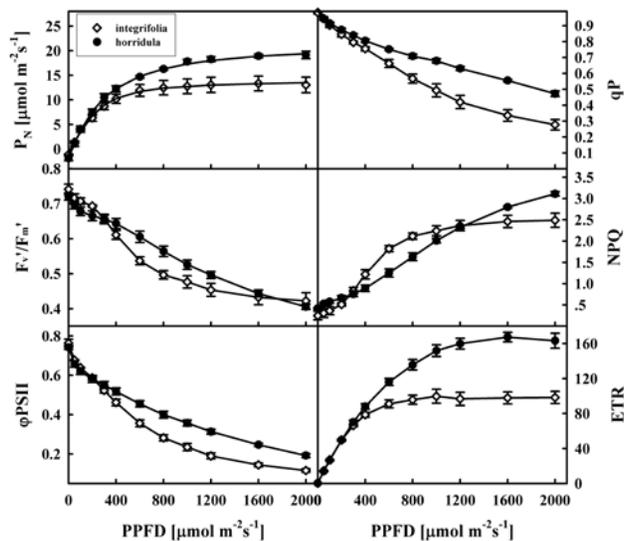f photosynthetic performance. At ambient condition, the F_v/F_m values of both species were not significantly different (Figure 2). Howeve, after exposure to 2000 μmol $m^{-2}s^{-1}$ PPFD for 30 min, the decrease in F_v/F_m of *M. integrifolia* was more pronounced than in *M. horridula*. The F_v/F_m of *M. horridula* recovered from photo-inhibition more rapidly than in *M. integrifolia* in the dark.

Both *M. integrifolia* and *M. horridula* showed an initial increase in P_N as leaf temperature climbed above 10°C (Figure 3). The optimal temperature for photosynthesis (T_{opt}) was 23.8°C in *M. horridula*, and 21.7°C in *M. integrifolia*. *Meconopsis horridula* had higher T_{opt} relative
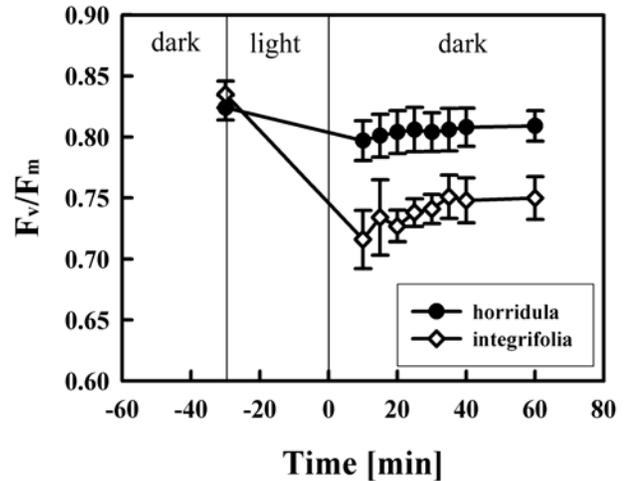
Figure 2. The maximum quantum yield of primary photochemistry of PSII in *Meconopsis horridula* and *M. integrifolia* monitored during the recovery period following a 30-min light stress treatment at 2000 μmol $m^{-2}s^{-1}$ PPFD. Each point represents the mean ± 1SE of three measurements.

Figure 1. Photosynthetic and chlorophyll fluorescence light response curves for *Meconopsis integrifolia* (◊) and *M. horridula* (●) at 360 μPa Pa^{-1} CO_2 concentration and 20°C leaf temperature. Each point represents the mean ± 1SE of three measurements.
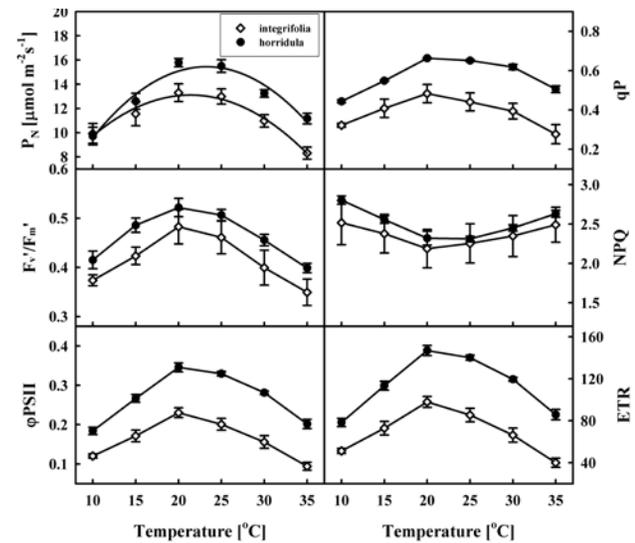
Figure 3. Effects of temperature on photosynthesis and fluorescence parameters of *Meconopsis horridula* and *M. integrifolia*. The measurements were conducted at a 1200 μmol $m^{-2}s^{-1}$ light intensity and a 350 μPa Pa^{-1} CO_2 concentration. Each point represents mean ± 1SE of three measurements.

to *M. integrifolia* (t=3.263, p=0.0282). The P_N at 10°C for *M. integrifolia* was 75.2% of the maximal value while for *M. hurridula* the P_N at 10°C was 62.4% of maximum. At 35°C, the P_N of *M. integrifolia* decreased to 63.4% of maximal value, and *M. horridula* to 70.8%. The maximal value of stomatal conductance (g_s) was found at 20°C in *M. horridula* and at 15°C in *M. integrifolia*. For both species, the g_s did not change significantly below 25°C, but it decreased above 25°C. The g_s at 35°C for *M. integrifolia* was 54.3% of the maximal value while the g_s at 35°C was 61.1% of the maximum in *M. horridula*. Although the two species showed the maximal values of F_v'/F_m', φPSII, qP and ETR about 20°C, the photochemical efficiency of *M. horridula* was higher than that of *M. integrifolia*. The lowest NPQ was found at 20°C for *M. integrifolia*, but at 25°C for *M. horridula*.

The photosynthetic CO_2 response curves indicated that *M. horridula* had a higher biochemical capacity (including V_{cmax} and J_{max}) for photosynthesis than *M. integrifolia* (Figure 4). At a C_i concentration of 520 µPa Pa⁻¹, the values of F_v'/F_m', φPSII, and ETR in *M. integrifolia* peaked and remained stable above this concentration while the values of F_v'/F_m', φPSII, and ETR in *M. horridula* peaked at a C_i concentration of 400 µPa Pa⁻¹ and decreased slightly above this C_i concentration. The qP value of *M. horridula* peaked at a lower C_i concentration than *M. integrifolia*. At a high C_i concentration, the NPQ values of the two species were similar, but that of *M. integrifolia* decreased from low C_i to high C_i concentration, the NPQ of *M. horridula* decreased to the lowest from 0 to 400 µPa Pa⁻¹ and then increased to 1600 µPa Pa⁻¹.

At saturating light, the P_N of *M. horridula* was higher than that of *M. integrifolia*. The higher P_{Nmax} in *M. horridula* was supported by greater V_{cmax} and J_{max}. *Meconopsis horridula* had higher g_s value than *M. integrifolia*, but the g_m of the two species was not significantly different. N content per leaf mass of two species revealed no significant differences while N content per leaf area in *M. horridula* exceeded that in *M. integrifolia* owing to the higher dry mass per unit area. The chlorophyll content per unit area in *M. horridula* was lower relative to that in *M. integrifolia* (Table 1).

DISCUSSION

Differences in photosynthetic performance and adaptation are both genetically determined and environmentally induced (Hamerlynck and Knapp, 1996). *Meconopsis horridula* showed higher light requirements and could recover from high-light inhibition more rapidly than *M. integrifolia*. The higher qP of *M. horridula* under high PPFD conditions indicated that its photo-protective
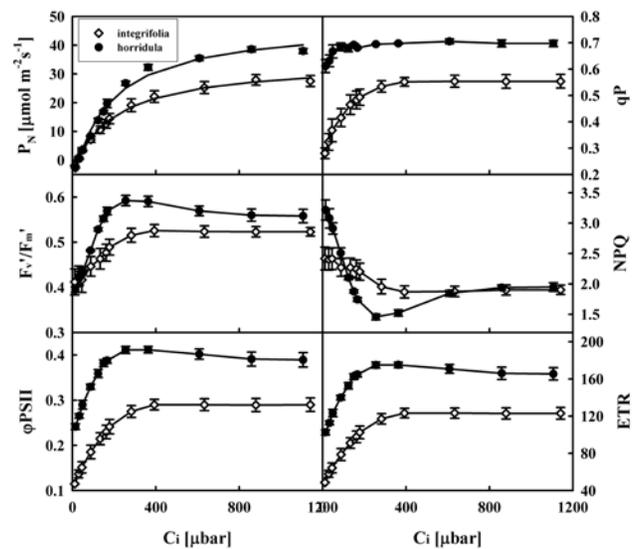

Figure 4. Photosynthesis and fluorescence parameters of *M. horridula* and *M. integrifolia* in response to intercellular CO_2 concentration at 1200 µmol m⁻²s⁻¹ light intensity and 20°C leaf temperature. Each data point represents mean ± SE of three measurements.

Table 1. Comparison of photosynthetic parameters and related leaf traits of *Meconospsis integrifolia* and *M. horridula*. Different letters indicate mean statistically different values p<0.05 as determined by t-test between species.

Parameters	*integrifolia*	*horridula*	t	p
P_{Nmax} (µmol m⁻²s⁻¹)	15.07±1.73[a]	23.40±1.42[b]	3.721	0.020
AQE (mol CO_2 mol photons⁻¹)	0.051±0.002[a]	0.065±0.010[b]	3.066	0.037
V_{cmax} (µmol m⁻²s⁻¹)	51.67±2.33[a]	113.33±15.32[b]	3.979	0.016
J_{max} (µmol m⁻²s⁻¹)	128.00±10.41[a]	228.67±5.24[b]	8.639	0.001
g_s (mol m⁻²s⁻¹)	0.154±0.004[a]	0.196±0.007[b]	3.979	0.016
g_m (mol m⁻²s⁻¹)	0.229±0.052[a]	0.209±0.057[a]	0.268	0.802
N_m (mg g⁻¹)	23.73±0.87[a]	26.18±1.01[a]	1.839	0.140
N_a (g m⁻²)	1.98±0.09[a]	4.62±0.23[b]	10.927	0.000
Chl (mg dm⁻²)	3.951±0.118[a]	2.647±0.069[b]	9.539	0.001
LMA (g m⁻²)	83.25±2.67[a]	176.49±5.13[b]	16.126	0.000

strategy seemed more efficient. A major contributor to the protection of the photosynthetic apparatus in plants growing in excess excitation energy is an increased ability to dissipate this energy via non-photochemical quenching such as the xanthophylls cycle, which is one of the mechanisms protecting chloroplasts from excess PPFD (Hjelm and Ögren, 2004). The NPQ of *M. integrifolia* increased rapidly below 1000 µmol m^{-2}s^{-1} and remained relatively constant, indicating that the lower NPQ would limit the photosynthetic performance under high light condition. This difference could be explained by the sharp spines on the stem and leaves of *M. horridula*, since their presence would reduce the absorbed light, thereby increasing the adaptation to high light. In addition, the lower chlorophyll content in *M. horridula* would reduce photon capture and avoid photo-damage by excess energy under high PPFD conditions.

Plants from habitats that differ in temperature regimes had different temperature response characteristics; such that the photosynthetic rate at temperatures close to their normal growth temperatures may be maximized (Cabrera et al., 1998). In the present study, *M. horridula* had a higher T_{opt} than *M. integrifolia*. The P_N of the former at high temperature was significantly higher than that of the latter. The difference in T_{opt} can reflect the influence of more hairs on the stems and leaves (Tsukaya and Tsuge, 2001). Across temperatures, stomatal conductance and photosynthetic rate in *M. horridula* (r^2=0.228, p=0.045) and *M. integrifolia* (r^2=0.236, p=0.041) enjoyed a close relationship. In particular, the reduced g_s above 25°C would exert an important effect on the inhibition of photosynthesis. NPQ is thought to be a good indicator of the concentration of dissipating complexes and the ability of plants to dissipate light energy in excess of that required for CO_2 assimilation (D'Ambrosio et al., 2006). Stress conditions such as high light or unfavorable temperatures markedly promote non-photochemical quenching. At moderate light intensity, non-photochemical quenching is dependent on the temperature (Bilger and Björkman, 1991). The variation in NPQ of *M. integrifolia* and *M. horridula* confirmed previous findings. The values of NPQ in the two *Meconopsis* species were increased to avoid photo-damage when exposed to unfavorable temperatures. Acclimating to different temperatures affected the growth of *Meconopsis* plants after growing at the lower altitude. Although the growth of *M. integrifolia* and *M. horridula* is limited by high summer temperatures (Ren, 1993), *M. horridula* had higher photosynthesis at high temperatures and might be better at tolerating them.

The electron transport rate (ETR) of the two *Meconopsis* species increased with increasing C_i, but the ETR of *M. horridula* above saturated C_i decreased slightly, while *M. integrifolia* remained constant. This indicated a triose phosphate utilization (TPU) limitation in *M. horridula*, but not in *M. integrifolia*. Triose phosphate utilization by end-product (sucrose, starch) synthesis may exert short-term feedback control of photosynthesis in the field at the extreme of source/sink imbalance before long-term adaptive mechanisms re-establish greater equilibrium. Hence the plants grown with CO_2 enrichment tend towards phosphate (P_i) limitation (Paul and Foyer, 2001). Low P_i reduces the capacity of the photosynthetic carbon reduction cycle to use nicotinamide adenine dinucleotide phosphate-oxidase (NADPH). Obviously, the electron transport rate is regulated by feedback (Sharkey, 1990), as excess electron transport capacity increases vulnerability to damage due to the formation of active oxygen species, particularly when exposed to environmental stress. Anything that restricts triose phosphate utilization can limit photosynthesis (Paul and Foyer, 2001). Short-term, low-temperature stress results in an inhibition of sucrose biosynthesis, which leads to a restriction in phosphate recycling and photophosphorylation. This is because the maximum capacity for triose phosphate utilization is temperature dependent, and chloroplast phosphate requirements increase at low temperature (Sage and Sharkey, 1987). Restriction in TPU would trigger feedback mechanisms that reduce the rate of photosynthetic electron transport, limit ATP supply, and thus reduce the rate of photosynthetic carbon assimilation. During the growing season at high elevation, the plants of *Meconopsis* frequently experience low temperatures (often below 10°C) at night, followed by high light and optimal temperatures during the day. As *M. horridula* had a weaker tolerance to low temperature than *M. integrifolia*, the triose phosphate utilization and photosynthetic electron transport in *M. horridula* would be suppressed by low temperature under high C_i conditions.

The variation in NPQ of *M. horridula* below 800 µPa Pa^{-1} was larger than that of *M. integrifolia*, indicating its greater sensitivity to CO_2. Golding and Johnson (2003) suggested that the electron transport is downregulated to match the reduced requirement for electrons when the CO_2 fixation is inhibited under low C_i conditions. Induction of NPQ at low C_i would quench the excess energy to minimize reactive oxygen production and alleviate the excitation pressure on PSII, as the pH gradient is needed to support the increase in NPQ. In the short-term, the restriction of P_i serves to increase the transthylakoid ΔpH gradient, preventing over-reduction of PSI and increasing energy dissipation (Paul and Foyer, 2001). As stomatal movement regulated by CO_2 concentration affects the entry of CO_2 into leaf and consumption of photosynthetic electron transport, the difference in the response of chlorophyll fluorescence to CO_2 is linked to stomatal conductance (Lawson et al., 2002).

Meconopsis horridula exhibited higher photosynthetic capacity and photochemical efficiency than *M. integrifolia* across all CO_2, light, and temperature levels examined. The cause of difference in photosynthesis among species is partly biochemical (Zhang et al., 2006). Leaf N content and photosynthetic capacity are strongly related because of the large proportion of leaf N present in the photosynthetic apparatus (Evans, 1989). Both N content per leaf area

(N_a) and N content per unit mass (N_m) were significantly correlated to light saturated P_N of two *Meconopsis* species (r^2=0.860, p=0.008; r^2=0.878, p=0.006, respectively). There was a positive correlation between N_a and V_{cmax} (r^2=0.897, p=0.004) or J_{max} (r^2=0.942, p=0.001). V_{cmax} is related to the content and activity of Rubisco while J_{max} is related to its regeneration. The higher leaf N content in *M. horridula* resulted in the higher Rubisco content and P_{Nmax}.

The low CO_2 partial pressure at high altitude would have a negative influence on photosynthetic CO_2 assimilation because CO_2 is the substrate for the carboxylation reaction of Rubisco (Körner, 1999). Some previous works on alpine plants showed that the negative impact of low CO_2 partial pressure on photosynthesis can be partly compensated for by the increase in diffusion of all gas-phase molecules at lower atmospheric pressure, and thus by the increased diffusion rates of CO_2 into the leaf (Smith and Donahue, 1991; Terashima et al., 1995). The photosynthetic capacities of alpine plants are not inferior to those of their lowland relatives (Körner, 1999; Zhang et al., 2007). Compared with the results of Shi et al. (2006), the values of P_{Nmax}, V_{cmax} and J_{max} in *M. horridula* were close to those of *Buddleja davidii* at a similar altitude. Shi et al. (2006) suggested that photosynthetic capacity is correlated with CO_2 diffusional conductance, and the decreasing temperature with increasing altitude affects CO_2 diffusion and the ratio of C_c to C_a.

Most of previous studies have shown that photosynthetic capacity is directly correlated with stomatal conductance and mesophyll conductance (Niinemets et al., 2005; Warren, 2006). *Meconopsis horridula* had higher g_s than *M. integrifolia*, but the g_m of the two species was not significantly different. The difference in P_{Nmax} was positively related to the stomatal conductance (r^2=0.758, p=0.024), but not mesophyll conductance (r^2=0.107, p=0.528). Thickness of leaf pubescence would increase leaf boundary layer resistance to CO_2 movement (Meinzer et al., 1985). Although the longer diffusive path found in thicker leaves increases resistance and thus reduces CO_2 concentrations at the sites of carboxylation (Kao and Chang, 2001), high LMA is often associated with higher amounts of mesophyll cell, N content, Rubisco content, and thereby photosynthetic rate (Friend and Woodward, 1990). The LMA of the two *Meconopsis* species was significantly related to P_{Nmax} (r^2=0.770, p=0.002).

In conclusion, *M. integrifolia* appeared to have a lower adaptive capacity to grow at lower altitudes because of fewer effective protective mechanisms against photo-inhibition. *Meconopsis horridula* was proven more resistant to photo-inhibition as it had more photosynthesis at higher temperatures and so might be relatively better at tolerating them. The capability of *M. horridula* to preserve the functional potential of the photosynthetic apparatus under heat stress conditions was probably an important factor in its capacity to grow and survive warmer habitats.

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全緣葉綠絨蒿和總狀綠絨蒿的光合適應性差異

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全緣葉綠絨蒿（*Meconopsis integrifolia*）和總狀綠絨蒿（*M. horridula*）原產於喜馬拉雅地區，是著名的觀賞和藥用植物。但是由於其難於忍受炎熱的夏季，在低海拔地方栽培綠絨蒿非常困難。為了探索適宜的栽培策略和預測引種栽培的植物表現，我們在海拔 3,260 米的苗圃內比較了全緣葉綠絨蒿和總狀綠絨蒿的光合作用能力及其光合作用對光照與溫度的反應。全緣葉綠絨蒿光合作用對高溫比總狀綠絨蒿敏感，而總狀綠絨蒿得到最大光合速率需要更高的光強。與全緣葉綠絨蒿相比，總狀綠絨蒿也表現出更高的飽和光合速率、最大羧化速率、飽和電子傳遞速率、氣孔導度、比葉重和單位面積葉氮含量，但它們的葉肉導度和單位重量的葉氮含量沒有顯著差異。兩種綠絨蒿的光合能力差異主要與其生化效率和葉片厚度相關，而與葉綠素含量和葉肉導度無關。研究結果表明，由於總狀綠絨蒿具有更寬泛的生理適應能力，它在低海拔地方的引種栽培比全緣葉綠絨蒿更易成功。

關鍵詞：綠絨蒿；光合作用；葉綠素螢光；葉片性狀；生理適應性。