



Flexible and reversible responses to different irradiance levels during photosynthetic acclimation of *Cypripedium guttatum*

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Summary

Cypripedium guttatum can be found both in open and shady habitats. Photosynthetic acclimation of *C. guttatum* to different light availabilities was detected using measurements of chlorophyll fluorescence, photosynthesis and leaf traits. When growing under low light conditions, *C. guttatum* exhibited a greater efficiency in photochemical utilization of absorbed light energy, and a lower ability for non-photochemical dissipation of excess light energy, as compared to the plants growing under high light conditions. Under intermediate light conditions, *C. guttatum* exhibited higher photosynthetic capacity (A_{\max}) than those under both low light or high light conditions. The differences in A_{\max} among three light environments was linked to the differences in biochemical efficiency, leaf N content (LNC) and leaf dry mass per unit area (LMA), but not to the differences of chlorophyll content. However, there were no significant differences in the light compensation points (LCP) and light saturation points (LSP) for photosynthesis for the plants growing under the three light conditions. These results indicate that the photosynthetic capacity of *C. guttatum* leaves allows for flexible and reversible responses to different irradiance levels. Photosynthetic acclimation in *C. guttatum* was affected by biochemical changes, the changes in LMA and ratio of Chl *a/b*. Successful acclimation of *C. guttatum* to a broad range of light levels likely allows for its wide

Abbreviations: A_{\max} , light-saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); AQE, apparent quantum efficiency ($\text{mol CO}_2 \text{ mol photons}^{-1}$); Chl *a*, chlorophyll *a* content (mg dm^{-2}); Chl *a/b*, ratio of chl *a/b*; Chl *a+b*, total chlorophyll content (mg dm^{-2}); Chl *b*, chlorophyll *b* content (mg dm^{-2}); ETR, apparent rate of electron transport of PSII; F_v/F_m , maximum photochemical efficiency of PSII; gs, stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$); HL, high light; J_{\max} , light-saturated rate of electron transport ($\mu\text{mol m}^{-2} \text{s}^{-1}$); LCP, light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$); LL, low light; LMA, leaf dry mass per unit area (g m^{-2}); LNC, leaf nitrogen content (g m^{-2}); LSP, light saturation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$); ML, medium light; qNP, non-photochemical quenching coefficient; qP, photochemical quenching coefficient; RSL, relative stomatal limitation; T_{opt} , optimum photosynthetic temperature ($^{\circ}\text{C}$); V_{cmax} , maximum RuBP saturated rate of carboxylation ($\mu\text{mol m}^{-2} \text{s}^{-1}$); ΦPSII , quantum yield of PSII

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geographical distribution. A level of about 45% sunlight appears to be optimal for photosynthesis.

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Introduction

Changes in light environments can have important impacts on a plant's photosynthetic apparatus. Insufficient light may stress a plant by limiting photosynthesis, resulting in reduced carbon gain and growth. Conversely, high light levels may damage the photosynthetic apparatus (Pastenes et al., 2003). Accordingly, numerous strategies have evolved to deal with the effects of variation in light availability, such as increased photosynthetic efficiency and increased thermal dissipation. Photosynthetic acclimation to changing light conditions is usually associated with anatomical as well as physiological changes within leaves (Boardman, 1977; Evans and Poorter, 2001; Lin and Hsu, 2004). However, the capacity for photosynthetic acclimation is species-specific. For example, three species of the genus *Illicium* have similar A_{\max} in either shade or full sun, while other species in this genus experience a significant reduction in A_{\max} in full sun (Griffin et al., 2004). The capacity for photosynthetic acclimation is also linked to habitat distribution (Murchie and Horton, 1997). It is likely that acclimation is important in optimizing resource allocation, and provides a competitive advantage in changing environments.

Cypripedium guttatum SW. is the most widely distributed slipper orchid and the only species of the genus *Cypripedium* occurring in both the Old and the New World. In the Hengduan Mountains, it grows over a broad range of light levels, from deep shade to full sun. This species is well-known not only as ornamental plant, but also its stem and rhizome is also used medicinally (Cribb, 1997). In recent years, the collection for illicit trade has resulted in considerable decline of *Cypripedium* populations (Cribb and Sandison, 1998).

Cypripediums are slow-growing plants that often need very specific and limited conditions for seed germination and offspring production (Kull, 1998). As a result, large-scale cultivation under artificial conditions is necessary for their conservation and for continued use in the ornamental trade. However, successful cultivation and conservation of wild species requires knowledge of their requirements for optimal growth (Lin and Hsu, 2004). Photosynthesis is widely used as a tool for indicating environmental stress and selection of growth

conditions suitable for different species (Pastenes et al., 2003; Lin and Hsu, 2004). It has been commonly observed that the capacity of plants to grow and develop in regimes differing from their original habitats depends on their ability for photosynthetic acclimation to changing environment (Percy, 1977). To date, however, there are few studies on domestication and cultivation of *Cypripedium* (Kull, 1999; Zhang et al., 2005). Indeed, although *Cypripediums* have been cultivated for centuries, and seedling micro-propagation has been successful for several members of genus *Cypripedium* (Cribb, 1997; Shimura and Koda, 2004), cultivation is still difficult because the optimal growing condition remains unclear.

One of the most important centers of distribution of the genus *Cypripedium* is the Hengduan Mountains of Southwestern China (Cribb, 1997). In this area, many forest ecosystems have been fragmented by logging and other human disturbance, resulting in a highly fragmented landscape. One important consequence of habitat fragmentation is an increase in irradiance on the understory plants. The increasing irradiance under habitat fragmentation may have important effects on physiology and anatomy of *C. guttatum* and therefore on its potential for growth and survival. However, the effects of different light intensity on the physiology and anatomy of *C. guttatum* is not well understood.

In this study, the photosynthetic characteristics and leaf traits of *C. guttatum* were investigated in three natural habitats with differing levels of light availability. Specifically, the objectives were to (1) assess the capacity for photosynthetic acclimation of *C. guttatum* to different light environments, and (2) to determine the optimal light requirements for growth. This information is necessary to ensure effective cultivation and conservation of *Cypripediums*.

Materials and methods

Plant material and sites

C. guttatum SW. is found in grasslands, open woodland and forest edges, at altitude of 1000–4100 m a.s.l. However, in the Hengduan Mountains it only occurs above 2700 m. *C. guttatum*

Table 1. Description of the sites used for the study of photosynthetic acclimation of *Cypripedium guttatum*

Site	Longitude	Latitude	Altitude (m)	Habitat	Light availability (% of full sunlight)	Soil N content (%)	Soil organic matter (%)
A (HL)	E 99°33.46'	N 27°55.28'	3350	Open wood	76	0.370	7.67
B (ML)	E 99°50.10'	N 27°47.76'	3450	Thicket	45	0.322	8.38
C (LL)	E 99°57.75'	N 27°36.57'	3360	Forest	22	0.347	7.07

Light availability was measured using a digital plant canopy imager (CI-110, CID, USA) at midday.

has two obovate, plicate leaves near the top of the stem. In the Hengduan Mountains, the growing period is about 140 d in a year and flowers appear in late May–July. The plant sets fruit between June and September, and becomes dormant in early October.

The study was conducted in three natural habitats with different light availabilities due to differences in canopy cover. The details of three sites were given in Table 1. The three sites have similar climatic conditions as the altitudinal and lateral distances between them are small. In this area, annual mean temperature and annual precipitation are 5.4 °C and 624.8 mm, respectively.

Analysis of chlorophyll fluorescence

Chlorophyll fluorescence was measured with a FMS-2 pulse modulated fluorometer (Hanstech, UK) in the early morning from June 8 to 12, in 2003. The minimal fluorescence (F_0) was determined by a weak modulated light, and a 0.8 s saturating light of $8000 \mu\text{mol m}^{-2} \text{s}^{-1}$ was used on the dark-adapted leaves (30 min) to determine the maximal fluorescence (F_m). Then the leaf was illuminated by an actinic light of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$. After 5 min, the steady-state fluorescence (F_s) was recorded and a second 0.8 s saturating light of $8000 \mu\text{mol m}^{-2} \text{s}^{-1}$ was given to determine the maximal fluorescence (F_m') on the light-adapted leaves. Ten leaves were measured at each site. The following parameters were calculated: (1) $F_v/F_m = (F_m - F_0)/F_m$; (2) $\Phi\text{PSII} = (F_m' - F_t)/F_m'$; (3) $\text{ETR} = \Phi\text{PSII} \times \text{PAR} \times 0.85 \times 0.5$, where 0.5 was a factor assuming an equal distribution of absorbed photons between PSI and PSII, and leaf absorbance was taken as 0.85; (4) $qP = (F_m' - F_s)/(F_m' - F_0)$; (5) $qNP = 1 - (F_m' - F_0)/(F_m - F_0)$ (Maxwell and Johnson, 2000; Pastenes et al., 2003).

Measurement of gas exchange

Diurnal photosynthetic variations were measured on five fully expanded leaves from 08:00 a.m. to

18:00 p.m. on clear days in June 2003 (flowering period). After steady state of gas exchange had been achieved, photosynthetic rate (A), leaf temperature (T_l), transpiration rate (E) and photosynthetic active radiation (PAR) were measured using a portable infra-red gas exchange system with a leaf chamber type PLC-B (CIRAS-1, PP Systems, UK). Meanwhile, a data logger (Li-1400, Li-Cor, USA) was used to record irradiance, air temperature and relative air humidity at hourly intervals. Leaf and air temperature and relative humidity were used to calculate vapor pressure deficit between leaf and air (VPD). Water use efficiency (WUE) was calculated as the ratio between A and E .

Photosynthetic responses to light were measured on fully expanded leaves using a CIRAS-1 infrared gas analyzer under constant leaf temperature (20 °C) and CO_2 concentration ($350 \mu\text{mol mol}^{-1}$). After the initial measurement at $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, light intensity was increased to produce 10 subsequent light levels at which photosynthetic rates were recorded. Three plants were measured at each site. Data were fit by a non-rectangular hyperbola (Prioul and Chartier, 1977). Using this function, light-saturated photosynthesis (A_{max}), apparent quantum efficiency (AQE), light compensation point (LCP) and light saturation point (LSP) were estimated by Photosyn Assistant software (v 1.1, Dundee Scientific, UK).

Following A-PAR response curves, A- C_i response curves were generated using a CIRAS-1 infra-red gas analyzer. At each site, three recently matured leaves were placed in the leaf chamber at CO_2 concentration of $350 \mu\text{mol mol}^{-1}$, 20 °C and $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR. Following a 15 min acclimation period, the photosynthetic rate was recorded, then the CO_2 concentration was reduced to $50 \mu\text{mol mol}^{-1}$ and another reading was taken. A gradual increase in ambient CO_2 to a final concentration of $2000 \mu\text{mol mol}^{-1}$ in 10 increments was carried out, with a reading taken at each increment following a 3 min acclimation period. Using the A- C_i curves, the maximum carboxylation rate by Rubisco (V_{cmax}) and light-saturated electron transport

(J_{\max}) were calculated by Photosyn Assistant software that applied the biochemical model described by von Caemmerer and Farquhar (1981). Relative stomatal limitation (RSL) of photosynthesis was calculated from A-Ci curves by the method of Farquhar and Sharkey (1982).

The dependence of photosynthesis on temperature was examined on fully expanded leaves using an infrared gas analyzer in the morning to avoid high temperatures at midday. Measurements were made between 10 and 35 °C at CO₂ concentration of 350 $\mu\text{mol mol}^{-1}$ and PAR 600 $\mu\text{mol m}^{-2}\text{s}^{-1}$. A second-order polynomial equation was used to fit optimum photosynthetic temperature.

Analysis of leaf traits

Following the measurements of photosynthetic response, the leaves were harvested from the sampled plants. In the laboratory, leaf areas were measured using a leaf area meter (LI-3000A, USA). Dry mass was determined after drying for 48 h at 70 °C. Then, leaf N content was analyzed using a N analyzer (LecoFP-428, USA). LMA was calculated as leaf dry mass per unit area (g m^{-2}). Chlorophyll was extracted by 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). Three replicates were made for each site.

Statistical analysis

Statistical analysis was performed using SPSS 10.0 (SPSS Inc., Chicago, USA). To estimate the differences among different sites, the values of chlorophyll fluorescence, photosynthetic parameter and leaf trait were tested using one-way ANOVA and LSD multiple comparisons tests. The relationships between photosynthetic parameters and leaf traits were assessed using linear regression analysis.

Results

Diurnal variations in environmental factors and gas exchange

The diurnal variations of PAR, T_l and VPD showed similar trends during the day at the three sites (Fig. 1). They increased rapidly after 8:00 a.m., reaching maximum values between 12:00 a.m. and 14:00 p.m. The high light (HL) site had higher PAR values than those at medium light (ML) and low

light (LL) sites ($F = 12.559$, $P = 0.000$). The higher PAR in the HL site resulted in the higher VPD and T_l ($F = 6.06$, $P = 0.003$) during the day.

The maximum values of g_s occurred in the early morning, decreased toward midday and increased in the afternoon (Fig. 1). The diurnal variation of g_s was opposite to that of VPD. There was no significant difference in g_s under three light environments ($F = 2.403$, $P = 0.094$). However, the daily mean C_i values of plants were significantly different among three sites ($F = 25.856$, $P = 0.000$). The maximal value of transpiration rate was observed around noon. The plants from HL site had a higher daily mean E than those in the LL sites ($F = 7.317$, $P = 0.001$).

The average photosynthesis of *C. guttatum* growing in the three light environments increased rapidly with the increasing PAR after 08:00 a.m. (Fig. 1), reaching maximum values at 11:00 a.m., and no midday depression of photosynthesis was found. The ML and HL plants leaves had higher mean photosynthesis (A_{day}) than that of the LL plants ($F = 4.557$, $P = 0.012$), while there were no significant differences in A_{day} between HL and ML plants ($P = 0.342$). HL plants had the lowest WUE ($F = 3.797$, $P = 0.024$), while the WUE of ML plants was similar to that of LL plants ($P = 0.758$).

Photosynthetic responses to temperature, PAR and C_i

C. guttatum plants growing in the three light environments showed no significant differences in optimal temperature of photosynthesis ($F = 0.697$, $P = 0.534$) (Fig. 2a). The plants attained highest photosynthetic rates at 20–21 °C (Table 2). Under all three light environments, photosynthetic rates remained in excess of 90% of maximum between 13 and 28 °C.

C. guttatum leaves exhibited also similar responses to light in three light environments (Fig. 2b). Although LSP increased with increasing light intensity, there were no significant differences in LSP ($F = 0.447$, $P = 0.659$) and LCP ($F = 0.471$, $P = 0.646$) among the three light conditions. Light saturation occurred between 528 and 608 $\mu\text{mol m}^{-2}\text{s}^{-1}$ PAR. ML plants had the highest light-saturated photosynthesis (A_{\max}), while LL plants had the lowest ($F = 12.411$, $P = 0.007$). However, this difference was not significant. The AQE of ML plant was higher than those of LL plant and HL plant (Table 2).

The dependence of photosynthesis on intercellular CO₂ concentrations in *C. guttatum* was shown in Fig. 2c. *C. guttatum* growing under ML conditions

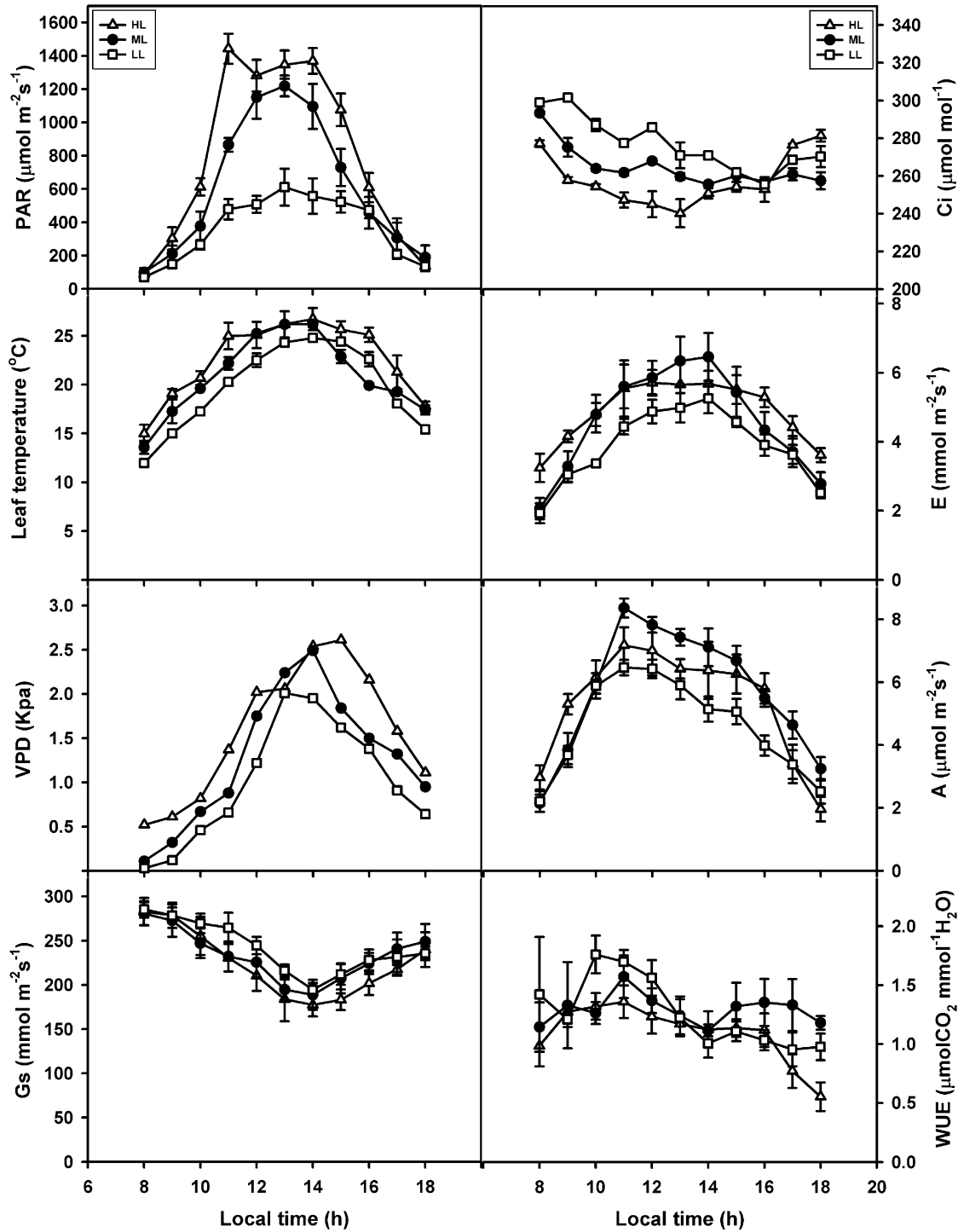


Figure 1. Diurnal variation in photosynthetic active radiation (PAR), leaf temperature, vapor pressure deficit (VPD), stomatal conductance (gs), intercellular CO₂ concentration (C_i), transpiration rate (E), photosynthetic rate (A) and water use efficiency (WUE) for *C. guttatum* under high light (Δ), medium light (●) and low light (□) environment. Each point is the mean of five measurements. Error bar represents $\pm 1SE$.

had the highest values of V_{cmax} and J_{max} (Table 2). However, there was no significant difference in RSL among three sites ($F = 4.545$, $P = 0.288$). In addition, RSL of *C. guttatum* was not significantly related to A_{max} ($R^2 = 0.011$, $P = 0.785$).

Differences in chlorophyll fluorescence under different light conditions

F_v/F_m , $\Phi PSII$, qP and ETR are related to photochemical processes, while qNP are related to

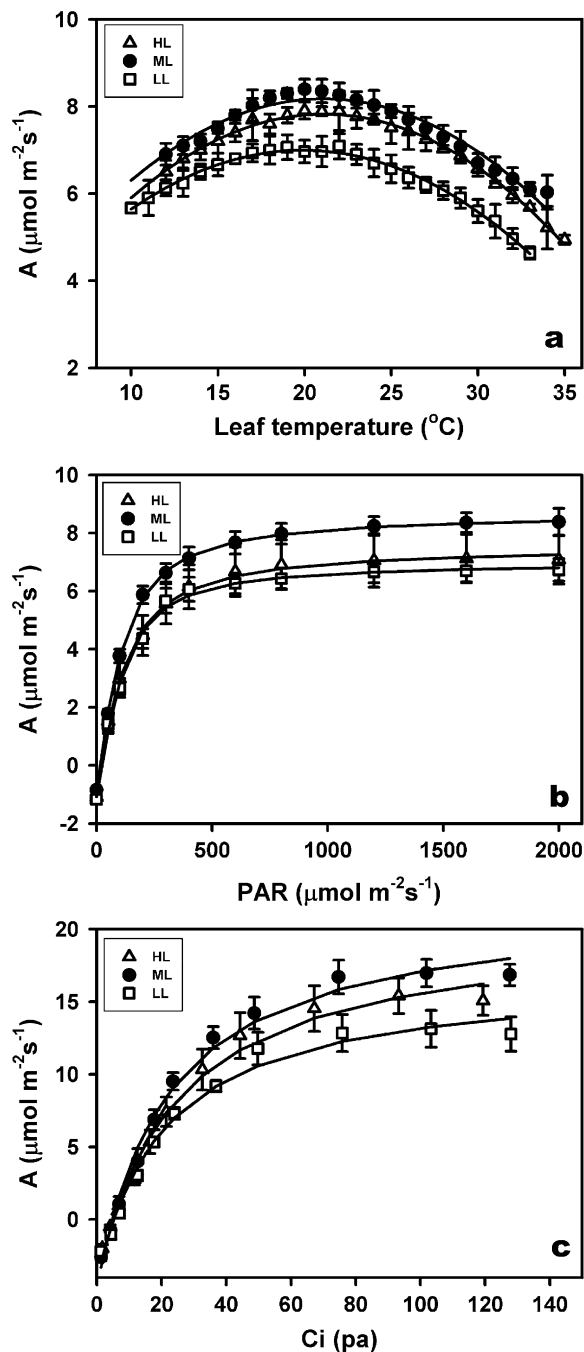


Figure 2. Photosynthetic response of *C. guttatum* growing under high light (Δ), medium light (\bullet) and low light (\square) environments to temperature (a), light (b) and CO_2 (c). Each point is the mean of three measurements. Error bar represents $\pm 1\text{SE}$.

non-photochemical processes (Fig. 3). These values are sensitive to differences in the light environment. When *C. guttatum* plants were exposed to high light, the values of F_v/F_m decreased ($F = 6.238$, $P = 0.004$), indicating that HL plants would be stressed by excess irradiance. The HL plants also had lower photochemical yields than LL

plants. The values of ΦPSII ($F = 7.830$, $P = 0.001$) and qP ($F = 130.077$, $P = 0.000$) for *C. guttatum* decreased greatly with increasing irradiance, but the ETR increased ($F = 3.903$, $P = 0.028$). There was an increase in qNP ($F = 17.854$, $P = 0.000$) with increasing growth irradiance, which indicated that the light energy absorbed by *C. guttatum* leaves growing under HL condition exceeded the capability of the photosynthetic apparatus to transform it into chemical energy, and thermal dissipation increased.

Leaf traits under different light conditions

The chlorophyll content per unit area for *C. guttatum* decreased with increasing irradiance, the plants growing under LL condition had higher total chlorophyll content than that under HL condition (Table 2). In contrast, there were dramatic increases in Chl a/b ratio with the increasing irradiance ($F = 9.631$, $P = 0.013$). The leaf N content per unit area (LNC) of *C. guttatum* growing in the ML site was higher than that at the HL and the LL sites ($F = 5.659$, $P = 0.042$). LMA increased with increase in light availability ($F = 6.474$, $P = 0.032$) and there was a significant difference in LMA between LL and HL plants (Table 2).

Discussion

Sunlight is one of the major environmental factors influencing photosynthesis, growth and reproduction of understory plants (Zhang et al., 2005). This study illustrates that photosynthesis of *C. guttatum* is also influenced by irradiance levels. Photosynthetic rates at light saturation (A_{max}) differed significantly across the three sites, with plants growing in the ML site having higher A_{max} than those under LL and HL conditions. While these results are consistent with those found for some species (Zhang et al., 2003), other studies have recorded photosynthetic rates in HL conditions to be higher than those under LL conditions (Boardman, 1977). Our findings for *C. guttatum* could be due to the partial photoinhibition of *C. guttatum* under very high irradiance (Zhang et al., 2003).

Changes in the Chl a/b ratio are related to the balance of the light absorption capacity of these two photosystems (Kitajima and Hogan, 2003). Typically, HL plants have lower chlorophyll content than LL plants, but have higher Chl a/b ratios. Increasing Chl a/b ratios are in turn, associated with decreases in the size of the PSII light-harvesting antenna, and with changes in Rubisco (Evans

Table 2. Comparisons of photosynthetic parameters and leaf traits of *Cypripedium guttatum* growing in three different light levels

	Light availability			<i>F</i>	<i>P</i>
	HL	ML	LL		
A_{\max}	8.603 ± 0.108a	9.553 ± 0.186b	8.133 ± 0.289a	12.411	0.007**
AQE	0.058 ± 0.011a	0.064 ± 0.004b	0.052 ± 0.001c	7.588	0.023*
RSL	18.29 ± 4.63a	12.57 ± 0.95a	12.14 ± 0.75a	1.545	0.288
$V_{c\max}$	23.70 ± 0.45ab	25.93 ± 0.79b	21.30 ± 1.10a	7.944	0.021*
J_{\max}	90.47 ± 2.10ab	118.13 ± 14.05b	75.83 ± 3.98a	6.360	0.033*
gs	241.85 ± 5.06a	233.02 ± 5.86a	223.75 ± 6.52a	2.403	0.094
LCP	21.57 ± 3.73a	16.77 ± 1.52a	19.57 ± 7.91a	0.471	0.646
LSP	608.2 ± 33.5a	547.8 ± 85.5a	527.8 ± 57.8a	0.447	0.659
T_{opt}	20.83 ± 0.47a	20.73 ± 0.48a	20.13 ± 0.41a	0.697	0.534
LMA	59.83 ± 1.55a	58.30 ± 1.72a	49.99 ± 2.77b	6.474	0.032*
Chl <i>a</i>	1.463 ± 0.092a	1.587 ± 0.078a	1.643 ± 0.073a	1.281	0.344
Chl <i>b</i>	0.377 ± 0.035a	0.440 ± 0.040ab	0.507 ± 0.026b	3.566	0.095
Chl <i>a+b</i>	1.840 ± 0.125a	2.027 ± 0.117ab	2.150 ± 0.085b	2.003	0.216
Chl <i>a:b</i>	3.913 ± 0.073b	3.643 ± 0.105b	3.257 ± 0.133a	9.631	0.013*
LNC	0.763 ± 0.026a	0.853 ± 0.019b	0.707 ± 0.043a	5.659	0.042*

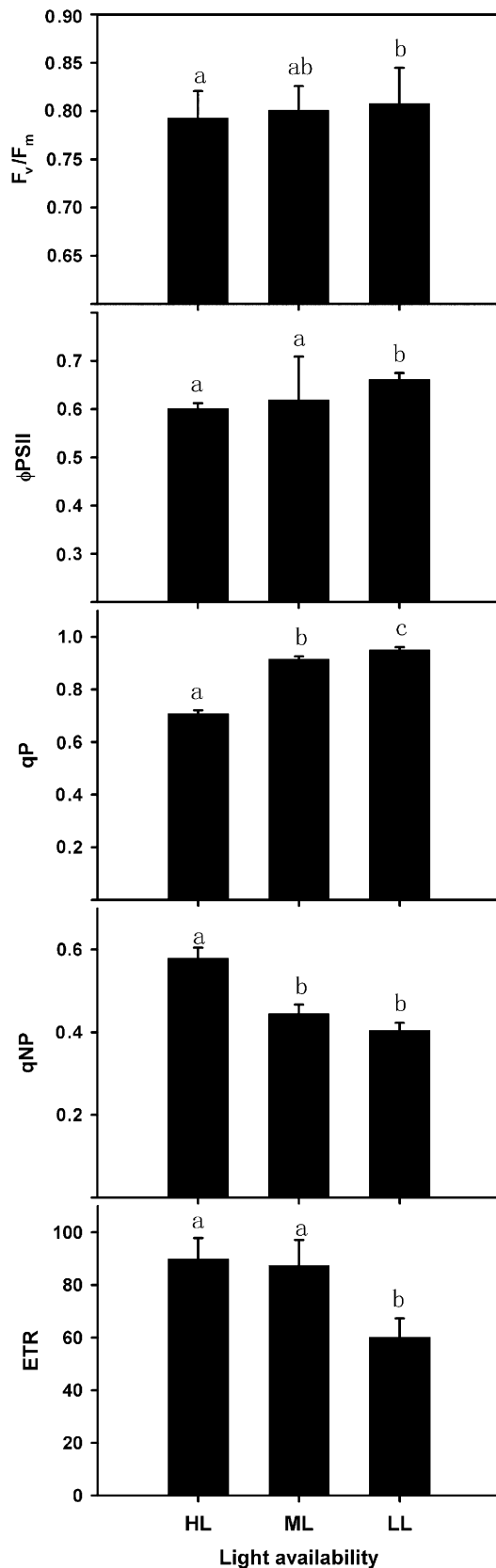
Data represent means ± SE and were analyzed with one-way ANOVA. Within each row, different letters indicate statistically significant differences between light levels Ns, * $P < 0.05$ and ** $P < 0.01$.

and Poorter, 2001). This study is consistent with the above, as the Chl *a/b* ratio in *C. guttatum* increased with increasing light intensity.

In addition, plants beneath a canopy are inescapably subjected to the reduction of light quantity and alteration of light quality due to reflection and selective absorption by the leaves of upper canopy. In general, comparing with those in open habitats, the level of green light under canopy is higher, and the levels of both red light and its proportion to far red light are lower. The change in light quality was correlated with the vegetation height and density (Skálová et al., 1999). This indicates that the incident light reaching the plants of *C. guttatum* grown under LL condition had higher R:FR ratio comparing with those under HL condition. It is believed that light quantity represents the changes in resource availability, while light quality acts as a source of information and can prompt morphogenetic responses (Stuefer and Huber, 1998). However, evidences in the literatures suggested that photosystem stoichiometry and photosynthetic characteristics would be affected by light quality (Chow et al., 1990; Turnbull, 1991). The efficiency of photosynthetic electron transport depends on the coordinated interaction of PSII and PSI in the electron-transport chain. Each photosystem is associated with distinct pigment-protein complex, which absorbs the light in different wavelengths. The adjustment in photosystem stoichiometry in chloroplast can correct the unbalanced absorption of light by two photosystems and

optimize electron transport, thereby improving photosynthetic efficiency (Chow et al., 1990; Walters, 2005). The ratio of Chl *a/b* is a reliable indicator of the proportion of LHCII to other Chl-containing complexes (Murchie and Horton, 1997). The ratio of Chl *a/b* in *C. guttatum* grown under LL condition was significantly lower than those under HL and ML conditions, suggesting the LL plants had a higher ratio of PSII to PSI. Under LL condition, a higher ratio of PSII/PSI may ensure that the supply of electrons from PSII is sufficient to keep pace with the rate of excitation of PSI so that light reaching PSI is efficiently used. Conversely, under HL condition a decreased PSII/PSI ratio may keep the rate of PSI and PSII excitation balanced, so that absorbed light is efficiently used (Walters, 2005). The alterations in the ratio of Chl *a/b* of *C. guttatum* under different light conditions would be adjusted jointly by light quantity and light quality. Such adjustment is a compensation strategy designed to correct unbalanced absorption of light by two photosystems for either improving photosynthetic efficiency or decreasing photodamage under changing light conditions (Chow et al., 1990).

With the increasing irradiance, LMA of *C. guttatum* increased. High LMA is often associated with higher mesophyll thickness and conductance, LNC and photosynthetic rate (Sims and Pearcy, 1992). However, *C. guttatum* plants growing under the differing light conditions did not differ in RSL or gs, and neither of these was related



to A_{\max} or LMA. The lower C_i in *C. guttatum* could be due to its higher photosynthetic rate in the HL condition (Von Caemmerer and Farquhar, 1981).

In general, LNC of sun leaves is higher than that of shade leaves and a strong positive correlation between A_{\max} and LNC is widely recognized (Warren and Adams, 2001). Here, *C. guttatum* leaf N content was significantly related to A_{\max} , J_{\max} and $V_{c\max}$. For *C. guttatum* growing under HL conditions, higher LNC appears to be an important determinant of higher A_{\max} . Under LL conditions, the limited N was likely invested in chloroplast components which resulted also in a lower rate of photosynthesis (Evans and Pooter, 2001).

The light energy absorbed by a leaf can be consumed by photochemical processes and non-photochemical processes. With increasing light intensity, the proportion of excess light energy increases. Excess light energy can cause photoinhibition and photodamage under HL conditions. *C. guttatum* grows understory of the forest and the A-PAR response curves measured by photosynthetic gas exchange illustrated that photosynthesis of *C. guttatum* leaves saturated at PAR of 500–600 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Moreover, the LSP did not differ significantly among the sites with different light levels. Under HL conditions (72% of full sun), the light intensity exceeded 1400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at midday. Although the F_v/F_m of HL plants was lower than that of the LL plants, it was close to 0.8 which is typical of healthy, non-photoinhibited leaves (Maxwell and Johnson, 2000). This suggests that the PSII reaction center functioned normally and that the level of photoinhibition was not high when *C. guttatum* was growing under HL conditions. This species exhibited a strong capacity for acclimation to a wide range of light environments. The lower photosynthetic rate and photochemical yield observed in plants growing under HL conditions could be ascribed to partial photoinhibition and the partial closure of PSII reaction (Zhang et al., 2003). Higher PAR caused not only an increase in leaf temperature but also an increase in VPD. The increase in leaf temperature alone due to direct sunlight could exacerbate photoinhibition. It also could exacerbate possible water stress leading to photoinhibition through the reduction

Figure 3. Comparisons of maximum quantum efficiency of PSII (F_v/F_m), quantum yield of PSII (Φ_{PSII}), photochemical quenching coefficient (qP), non-photochemical quenching coefficient (qNP) and electron transport rate (ETR) for *C. guttatum* in three different light environments. Vertical bars indicate standard errors of means for 10 measurements. Different letters represent significant differences (LSD-test, $P < 0.05$).

in photosynthetic quantum yield (Kitao et al., 2000; Pastenes et al., 2003).

The electron transport rate (ETR) was found to be closely related to the photosynthetic activity. Lower ETR resulted in a lower photosynthetic capacity for *C. guttatum* growing under low light conditions. Non-photochemical quenching has been described as the most common form of protection against excess light and is associated with xanthophyll cycle activity (Maxwell and Johnson, 2000). The values of qNP in HL plants were significantly higher than those of the LL and ML plants, and increased up to 0.58. It has been suggested that qNP values close to 0.5 are a threshold for long-term photoinhibition in many species and growth conditions (Pastenes et al., 2003). Therefore, the decrease in the F_v/F_m of *C. guttatum* leaves under HL conditions, which indicates a loss of the photochemical efficiency, is clearly correlated with low qNP values.

In conclusion, variations in the photosynthetic characteristics of *C. guttatum* growing in different light environments reflect physiological adaptations to changing light environments. The photosynthetic acclimation of *C. guttatum* to different levels of irradiation was correlated with changes in LMA, leaf N content, ratio of Chl *a/b* and thermal dissipation. Successful acclimation of *C. guttatum* to a broad range of light conditions likely allows for its wide geographical distribution. On the other hand, increased light intensity caused by forest fragmentation could decrease photosynthesis and growth of *C. guttatum*, as our results indicate that 45% full sunlight could be considered as the optimal condition for this species.

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