

Photosynthetic performances of transplanted *Cypripedium flavum* plants

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Abstract. To explore the conservation and cultivation of *Cypripedium flavum* at comparatively lower altitudes, a study on variations in photosynthetic characteristics was conducted on *C. flavum* plants from the high mountains of the eastern Himalayas. Plants of same size (6 leaves, 35-40 cm height) were selected from Tianshengqiao (alt. 3,450 m) and planted at the gardens at Zhongdian (alt. 3,200 m) and Kunming (alt. 1,900 m). The leaves of *C. flavum* at Tianshengqiao and Zhongdian exhibited higher photosynthetic rate, stomatal conductance, transpiration rate, apparent quantum yield, and carboxylation efficiency than their counterparts at Kunming. The optimal temperatures for photosynthesis of *C. flavum* plants growing at Tianshengqiao, Zhongdian, and Kunming were 18, 19 and 21°C, respectively. The optimal temperature also increased with increasing photosynthetically active radiation (PAR). However, the photosynthetic responses of *C. flavum* to PAR were similar at the three sites. The photosynthesis reached light saturation at the PAR of 746-832 $\mu\text{mol m}^{-2}\text{s}^{-1}$. The inability of *C. flavum* to acclimate to higher temperature resulted in the depression of photosynthetic rate at the lower altitude (Kunming). The results suggest that *C. flavum* adapts poorly to the warmer temperatures at low altitudes. It can be cultivated at a lower altitude, but proper agronomical methodology will need to be developed for better growth.

Keywords: Cultivation; *Cypripedium flavum*; Gas exchange; Optimal photosynthetic temperature; Photosynthetic capacity.

Introduction

The genus *Cypripedium* contains 49 species distributed in North America, East Asia, and Europe. The Hengduan Mountains are one of the most important distribution regions (Chen, 1985). *Cypripedium flavum* is a famous and rare alpine lady's slipper orchid that occurs in alpine grasslands or under the scrub and forest at altitudes of 2,700-3,700 m in the Hengduan Mountains (Fang, 1993). Because large-scale cultivation of this plant under artificial conditions is not economically feasible, wild populations of this species are the main source of material for horticulture. In recent years, ecological disturbance, unscientific and uncontrolled collection, tourism and increasing grazing pressure have resulted in considerable decline in the population number of *C. flavum* in the Hengduan Mountains (Cribb and Sandison, 1998; Huang and Hu, 2001). In order to meet the increasing demand for this species as an ornamental plant, commercial cultivation is necessary.

Strategies are being developed for the conservation and cultivation of *C. flavum* at lower altitudes. However, after transplanting from natural habitats to lower altitudes, *C. flavum* grows poorly (Weng et al., 2002), and the flower size shrinks. Previous studies showed that chilling treatment (4°C for 50 days) promotes the growth and flower-

ing of *Cypripedium* (Olver, 1981; Kim et al., 1996), but flowering of *Cypripedium* depends on plant size and vegetative growth (Primack and Stacy, 1998). In fact, the growth of plant often exhibits an optimum temperature. After transplanting to lower altitude, elevated temperature decreases the photosynthetic activity by impairing physiological processes. The reduction of photosynthetic carbon fixation directly affects vegetative growth and indirectly affects flowering through decreasing plant size and the supply of nutrition (Battaglia et al., 1996; McDonald and Paulsen, 1997; Totland, 1999; Prasad et al., 2000; Iersel, 2003; Griffin et al., 2004). Although *C. flavum* has been studied taxonomically (Lang, 1990; Cribb, 1997; Chen et al., 1998), studies of its physiology and cultivation that would assist in domestication are lacking (Kull, 1999). Information on physiological responses of this species to changed environments, such as growth at different altitudes, is needed for applied research aiming to increase the range of cultivation of alpine ornamental plants. The ability of species to acclimate and adapt to different environments is directly/indirectly associated with their ability to acclimate at the level of photosynthesis (Percy, 1977), which in turn affects biochemical and physiological processes of the leaf and, consequently, the physiology and growth of the whole plant (Chandra, 2003). Our aim, in this study, was to present basic information on the photosynthesis of *C. flavum* in its current habitat and to compare photosynthetic rates and factors affecting it at lower altitudes. We expect that this will assist in cultivation of this species at altitudes below its natural range.

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Materials and Methods

Study Sites and Plant Materials

The study was carried out at Tianshengqiao (alt. 3,450 m, 99°50' E, 27°49' N), Zhongdian (alt. 3,200 m, 99°38' E, 27°46' N), and Kunming (alt. 1,900 m, 102°41' E, 25°01' N), from May to June 2003. Tianshengqiao is a natural habitat of *C. flavum*, the others are mostly experimental gardens. These three sites have no obvious differences in latitude or day length, but the growing temperature is different. In Zhongdian, annual mean temperature and precipitation were 5.4°C and 624.8 mm (30-year mean), respectively. The rainfall and air temperature at Tianshengqiao are 4.2°C and 691.2 mm. Kunming has a mean annual temperature of 14.5°C and mean annual rainfall of 1035.3 mm (Figure 1) (Zhang, 1998; Weng et al., 2002).

Uniform seedlings (dormant) of *C. flavum* were collected at Tianshengqiao in the Hengduan Mountains in March 2002. These seedlings were transplanted into plastic cases (60×50×25 cm³) containing alpine soil from the natural habitat at Tianshengqiao. Fifteen cases (5-8 seedlings/case) of *C. flavum* were transplanted to plots in the Zhongdian and Kunming garden. To ensure the growth of seedlings was not influenced by the different soil, all plots contained the alpine soil from the natural habitat. The seedlings in Kunming and Zhongdian were shaded by nylon net to give 40-50% of full sunlight (similar to the light conditions in the natural habitat). They were watered regularly during dry periods. Irrigation was not required after the onset of monsoon rains. Sixty seedlings of similar size were marked for measurements at the natural habitat at Tianshengqiao.

Measurements of Photosynthetic Parameters

Photosynthetic parameters were measured during the flowering period in the following year (from May to June 2003), after one year of acclimation by seedlings at two new sites. As leaf emergence and the active growth period occurred slightly earlier at Kunming than at the other

locations, measurements of photosynthesis were first made at this location, followed by Zhongdian and then Tianshengqiao. At all sites, observations were recorded on fully mature healthy leaves (4th from base) of 60 randomly selected plants. This was then repeated thrice on different randomly selected plants and leaves at each site. All measurements were made between 9:00 and 11:00 am. Mean values were used in computations.

Photosynthetic responses to light were measured at 14 light levels on leaves at each study site using a CIRAS-1 infrared gas analyzer (PP system, UK). The CO₂ concentration in the leaf chamber was set to 350 μmol mol⁻¹, and temperature was 20°C. Sampled leaves were allowed to adapt to the PAR of 1000 μmol m⁻²s⁻¹ about 20-30 min before measurements. Preliminary measurements showed that this light intensity (1000 μmol m⁻²s⁻¹) was above the light-saturated point for *C. flavum*, but below the light intensity at which photoinhibition occurred. After the initial measurement at 0 μmol m⁻²s⁻¹, light intensity was increased to produce 13 subsequent light levels at which photosynthetic rates were recorded. The CO₂ response curves of photosynthesis were determined with a range of CO₂ concentrations (0-2000 μmol mol⁻¹) at a light intensity of 400 μmol m⁻²s⁻¹ and a temperature of 20°C. After the initial measurement at 2000 μmol mol⁻¹, CO₂ concentration was reduced to produce other subsequent levels at which photosynthesis was recorded. At each CO₂ concentration, the acclimation period was 2-3 min. Curve fitting software (Sigmaplot for Windows 8.0) was used to analyze both the Pn-Ci and Pn-PAR responses using a three-component exponential function of form (Watling et al., 2000).

$$P_n = a(1 - e^{-bx}) + C \quad (1)$$

where Pn = steady-state photosynthetic rate, and x = intercellular CO₂ concentration (Ci) or photosynthetically active radiation (PAR). Using this equation, the P_{max} (light-saturated photosynthetic rate at ambient CO₂ concentration) was calculated as a + c from Pn-PAR response curves. The carboxylation efficiency (CE) was estimated as the initial gradient of Pn-Ci curves (0-200 μmol mol⁻¹), and the apparent quantum yield (AQY) was calculated as the initial slope of Pn-PAR curves in the range of 0-400 μmol m⁻²s⁻¹ following Swanborough et al. (1997).

The dependences of net photosynthetic rate on temperature were examined with fully expanded leaves using a Ciras-1 infrared gas analyzer (PP system, UK) in the morning (between 8:00 and 11:00 am) to avoid high midday temperatures. During the measurement, the CO₂ concentration in the reference chamber was kept at 350 μmol mol⁻¹, relative humidity 60-70%, and 400 μmol m⁻²s⁻¹ PAR. The sequences of measurement began at 10°C and proceeded in 1°C increments until 35°C. At each temperature level, leaves were allowed to equilibrate for approximately 2 min before the readings were taken.

In the Zhongdian garden, at CO₂ partial pressure of 350 μmol mol⁻¹, the photosynthetic rates of *C. flavum* were measured under different temperatures at the PAR of 1800, 1400, 1000, 600 and 200 μmol m⁻²s⁻¹, respectively.

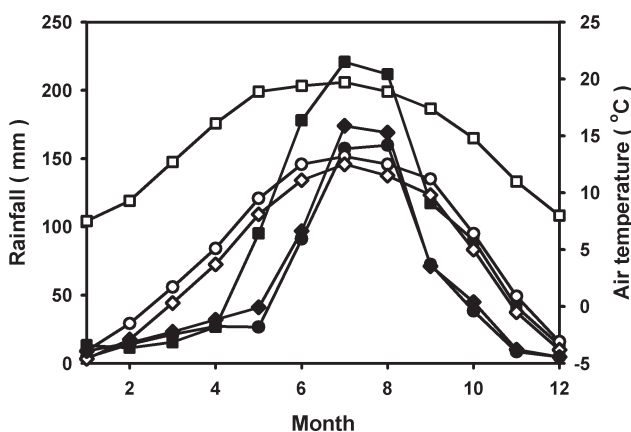


Figure 1. Seasonal variations of rainfall (Kunming: ■-■; Zhongdian: ●-●; Tianshengqiao: ◆-◆) and air temperature (Kunming: □-□; Zhongdian: ○-○; Tianshengqiao: ◇-◇) in Kunming, Zhongdian, and Tianshengqiao.

Statistical Analyses

Statistical analysis was performed using SPSS 10.0 for windows (SPSS Inc., USA). Differences between physiological variables were determined using analysis of variance (ANOVA) and LSD test for multiple comparisons.

Results

The temperature responses of photosynthesis at $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ PAR and a $350 \mu\text{mol mol}^{-1}$ CO_2 concentration of *C. flavum* were described by second-order polynomial curves (Figure 2). At different altitudes (sites), the growth temperature of *C. flavum* was different (Figure 1). Growth temperature had a significant effect on the temperature dependence of photosynthesis in leaves of *C. flavum* ($R^2 = 0.9542$, $n=26$). The photosynthetic optimum temperatures at Kunming, Zhongdian, and Tianshengqiao were 21, 19,

and 18°C , respectively. Photosynthetic rates remained in excess of 90% of maximum between 13.8 and 28.0°C at Kunming, between 13.5 and 26.5°C at Zhongdian, and between 11.0 and 25.0°C at Tianshengqiao. The main difference was that the seedling had a higher photosynthetic rate at higher altitudes (Zhongdian and Tianshengqiao) than at the lower altitude (Kunming) ($p < 0.001$). At the range of optimum temperature with $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ PAR and a $350 \mu\text{mol mol}^{-1}$ CO_2 concentration, the photosynthetic rate was 6.62 ± 0.074 , 7.633 ± 0.079 , $7.39 \pm 0.176 \mu\text{mol m}^{-2}\text{s}^{-1}$ at Kunming, Zhongdian, and Tianshengqiao, respectively.

The dependences of transpiration (E) and stomatal conductance (G_s) on leaf temperature were also determined at the same time as the photosynthesis measurements. Transpiration rate increased with increasing leaf temperature while stomatal conductance declined (Figure 2). However, all of these were lower at Kunming than those at Zhongdian and Tianshengqiao ($p < 0.01$).

The photosynthetic responses of *C. flavum* to temperature under different light intensities at Zhongdian showed significant differences (Figure 3) ($p < 0.05$). The optimal photosynthetic temperatures increased with increasing light intensity. They were 17.8 , 18.0 , 19.2 , 19.9 and 20.1°C under the photosynthetically active radiation (PAR) of 200, 600, 1000, 1400 and $1800 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. The photosynthetic rate at the PAR of $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$ was the highest of the five light intensities, followed by those at PAR of 600, 200, 1400, $1800 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. At the $200 \mu\text{mol m}^{-2}\text{s}^{-1}$ PAR, the photosynthetic rate of *C. flavum* declined rapidly above the optimal photosynthetic temperature. This indicated that low light intensity together with high temperature resulted in depression of photosynthesis in *C. flavum*.

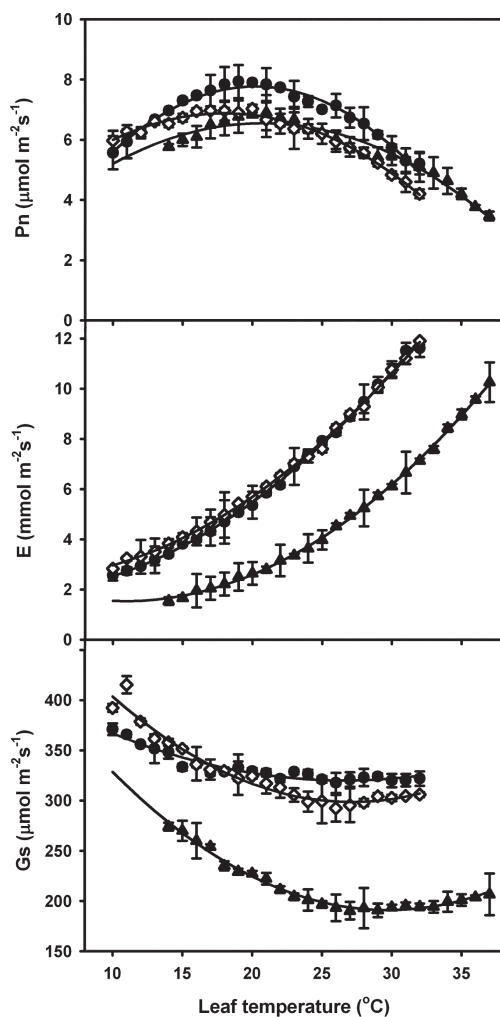


Figure 2. The effects of leaf temperature on net photosynthesis (P_n), transpiration rate (E) and stomatal conductance (G_s) of *C. flavum* at $400 \mu\text{mol m}^{-2}\text{s}^{-1}$ PAR and $350 \mu\text{mol mol}^{-1}$ CO_2 concentration at Kunming (\blacktriangle - \blacktriangle), Zhongdian (\bullet - \bullet), and Tianshengqiao (\diamond - \diamond). Vertical bars indicate standard errors of mean for three measurements.

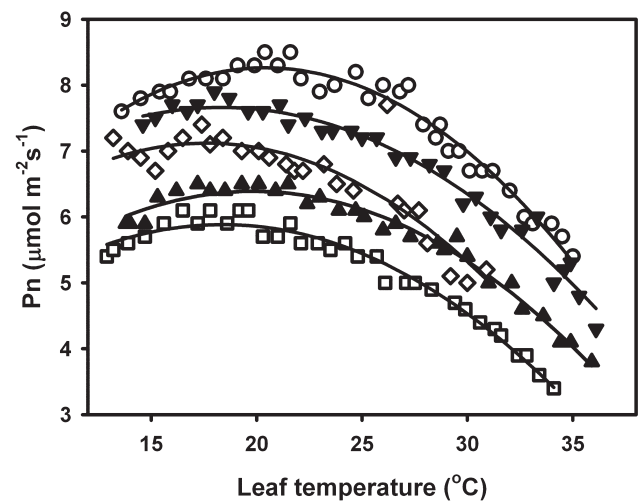


Figure 3. Effects of leaf temperature on photosynthetic rate under different irradiances ($1800 \mu\text{mol m}^{-2}\text{s}^{-1}$: \square - \square , $1400 \mu\text{mol m}^{-2}\text{s}^{-1}$: \blacktriangle - \blacktriangle , $1000 \mu\text{mol m}^{-2}\text{s}^{-1}$: \circ - \circ , $600 \mu\text{mol m}^{-2}\text{s}^{-1}$: \blacktriangledown - \blacktriangledown , $200 \mu\text{mol m}^{-2}\text{s}^{-1}$: \diamond - \diamond) at $350 \mu\text{mol mol}^{-1}$ CO_2 concentration at Zhongdian. Continuous lines are second-order polynomial curves of fit.

The photosynthetic responses to light at three sites are shown in Figure 4. Leaves of *C. flavum* at Kunming, Zhongdian, and Tianshengqiao became light saturated above 746.1, 793.2 and 832.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. However, the seedlings from Zhongdian and Tianshengqiao attained higher photosynthetic rates at saturating light levels than those at Kunming ($p < 0.05$). The quantum yield exhibited a trend similar to photosynthetic rate, with plants at higher altitudes using light more efficiently than those at lower altitudes (Figure 5) ($p < 0.05$). The photosynthetic compensation point of *C. flavum* at Kunming, Zhongdian, and Tianshengqiao were 25.2, 28.0 and 28.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. With the increasing light intensities, transpiration rates (E) of *C. flavum* at three sites increased while stomatal conductance (G_s) was similar at different light levels. However, both transpiration rate and stomatal conductance were lower at Kunming those than at Zhongdian or Tianshengqiao ($p < 0.01$).

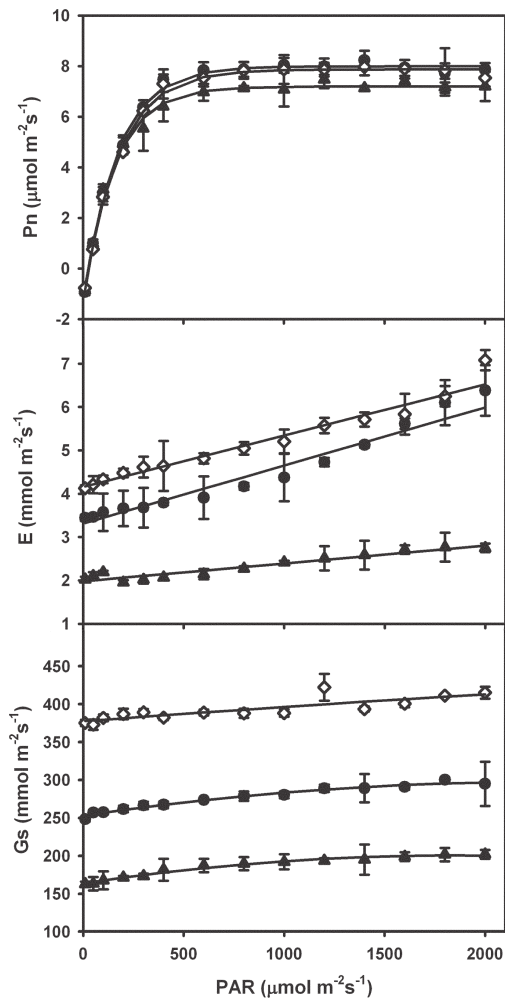


Figure 4. The dependences of net photosynthesis (P_n), transpiration rate (E) and stomatal conductance (G_s) of *C. flavum* on PAR at 20°C temperature and 350 $\mu\text{mol mol}^{-1}$ CO_2 concentration at Kunming (\blacktriangle - \blacktriangle), Zhongdian (\bullet - \bullet) and Tianshengqiao (\diamond - \diamond). Vertical bars indicate standard errors of mean for three measurements.

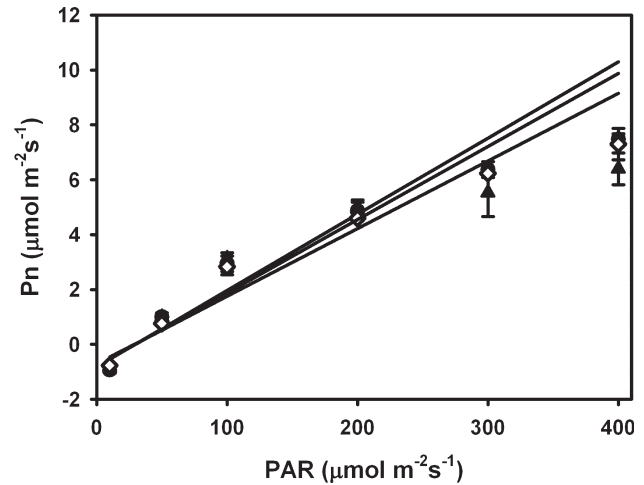


Figure 5. The initial slope of P_n -PAR response curves (quantum yields) of *C. flavum* at Kunming (\blacktriangle - \blacktriangle), Zhongdian (\bullet - \bullet) and Tianshengqiao (\diamond - \diamond). Vertical bars indicate standard errors of mean for three measurements.

The patterns of photosynthetic CO_2 response curves were similar at the three sites (Figure 6). The photosynthetic CO_2 compensation points at Kunming, Zhongdian, and Tianshengqiao were 91.9, 72.2 and 76.4 $\mu\text{mol mol}^{-1}$, respectively. The carboxylation efficiency (CE) was estimated as the initial slope of the P_n - C_i curves (0-220 $\mu\text{mol mol}^{-1}$). The carboxylation efficiencies of *C. flavum* at Zhongdian (0.0278 $\text{mol m}^{-2}\text{s}^{-1}$) and Tianshengqiao (0.0267 $\text{mol m}^{-2}\text{s}^{-1}$) were higher than at Kunming (0.0247 $\text{mol m}^{-2}\text{s}^{-1}$) ($p < 0.05$). This indicated that seedlings at higher altitudes had higher photosynthetic potentials than those at lower altitudes ($p < 0.01$). According to P_n -PAR response curves (Figure 4), the light-saturated photosynthetic rates of *C. flavum* at Kunming, Zhongdian, and Tianshengqiao were 7.19, 7.99 and 7.87 $\mu\text{mol m}^{-2}\text{s}^{-1}$, respectively.

Discussion

Generally, the variation in the photosynthetic rates reflected the adjustment to the growth environment (Rawat and Purohit, 1991). The light-saturated photosynthetic rates of *C. flavum* at Zhongdian (alt. 3,200 m, garden) and Tianshengqiao (alt. 3,450 m, natural habitat) were significantly higher than those at Kunming (alt. 1,900 m, garden) ($p < 0.01$), but there were no apparent differences between Zhongdian and Tianshengqiao ($p > 0.05$). Photosynthetic rate of different species differed in the response to altitudinal variation. The photosynthetic rates of some plants increased with increasing altitude (Rawat and Purohit, 1991) while others showed negative altitudinal patterns (Billings and Mooney, 1968; Cabrera et al., 1998). In our study, the photosynthetic rate of *C. flavum* increased with the increasing altitude. This difference may be related to adaptability of specific plant.

Cypripedium flavum was a typical alpine plant, and in its natural habitat at Tianshengqiao the optimum temperature for photosynthesis was 18°C. The monthly mean air

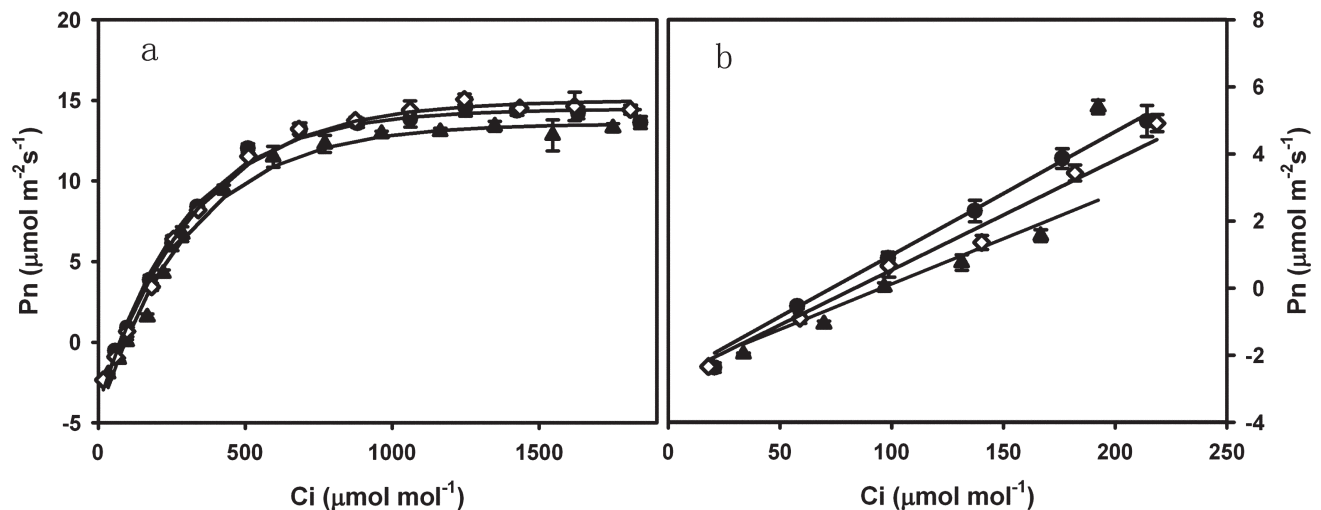


Figure 6. The dependences of Pn on intercellular CO_2 concentration at Kunming (\blacktriangle - \blacktriangle), Zhongdian (\bullet - \bullet) and Tianshengqiao (\diamond - \diamond) (a), and the initial slope of Pn- C_i response curves (carboxylation efficiency) of *C. flavum*. Vertical bars indicate standard errors of mean for three measurements.

temperatures from May to August were above 18°C at Kunming, and the day air temperatures were usually over 25°C (Figure 1). Daytime air temperatures at Kunming were obviously higher than, not only the photosynthetic optimum temperature of *C. flavum*, but also those of its natural habitat at Tianshengqiao. The inability of *C. flavum* to acclimate to higher temperatures resulted in the depression of photosynthetic rate at a lower altitude (Kunming), and it may suffer damage to its photosynthetic apparatus. Photosynthesis (especially PSII) is the most sensitive to high temperature damage among the plant functions. High temperature would cause reversible or irreversible damage to the photosynthetic apparatus (Berry and Björkman, 1980; Havaux, 1993; Pastenes and Horton, 1996; Braun et al., 2002; Salvucci and Crafts-Brandner, 2004). On the other hand, the stomatal conductance (G_s) of *C. flavum* at Kunming was significantly lower than those at Zhongdian and Tianshengqiao (Figure 2 and Figure 4). The lower G_s of *C. flavum* at the lower altitude reduced CO_2 into the leaf and water diffusion. Consequently, the photosynthetic rate and transpiration rate of *C. flavum* at Kunming were lower than those at Zhongdian and Tianshengqiao. In addition, the maximal photosynthetic rates of *C. flavum* at Zhongdian were slightly higher than at Tianshengqiao, the natural habitat. This can be attributed to the lack of strong environmental limitations in the garden, where conditions remained constant (Cordell et al., 1998).

The optimum temperature for photosynthesis of *C. flavum* was found to be around 20°C . Relatively higher temperature optima for photosynthesis have been reported for other alpine plants (Mooney and Billings, 1961; Körner, 1982), but these observations differed from ours in the Hengduan Mountains. The differences could be due to the original habitats of plants or different genetic makeup of the species (Rawat and Purohit, 1991; Terashima et al., 1993). The photosynthetic optimal temperature of *C. flavum* grown at a lower altitude (Kunming) seemed to be

higher compared to the seedling grown at a higher altitude (Zhongdian) and in its natural habitat (Tianshengqiao). Meanwhile the range of photosynthetic optimal temperature at Kunming was broader than ranges at the other two sites. When plants of the same species were grown at a lower altitude, a higher growth temperature caused an upward shift in the optimum temperature for photosynthesis (Mooney and West, 1964; Billings and Mooney, 1968).

The light saturation points of *C. flavum* grown at three sites were between 746 and $832 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 4). The highest rate of leaf photosynthesis occurred at the PAR $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ combined with 20°C leaf temperature (Figure 3). High temperature-high light intensity or low light intensity combined with high temperature adversely affected CO_2 assimilation in *C. flavum*.

In conclusion, the results of this study reveal that the adaptive potential of *C. flavum* photosynthesis to environmental conditions at lower altitudes is low. It can be cultivated at a lower altitude, but the proper agronomical methodology will be needed to be developed for better growth. The optimal growth conditions for *C. flavum* are 1/3-1/2 full sunlight with 15 - 25°C air temperature. If transplanted to lower altitude (e.g. Kunming), a good growth house will be necessary. In Zhongdian, the growth and photosynthetic rate of *C. flavum* under a simple nylon shade net were similar to those at its natural habitat. Therefore, it seems best to cultivate *C. flavum* plants at Zhongdian during its vegetative phase, and then transplant them to the lower altitude for flowering.

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引種黃花杓蘭的光合作用特性

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為保護並在低海拔地栽培黃花杓蘭，在 3 個實驗點對喜馬拉雅高山分佈黃花杓蘭的光合特徵進行了研究。相似大小植株采自于海拔 3,450 米的天生橋，在昆明（海拔 1,900 米）和中甸（海拔 3,200 米）進行栽培。經過一段時間適應後，於開花期對其氣體交換進行研究。天生橋（原生地）和中甸（引種地）的黃花杓蘭比昆明栽培的具有更高的光合速率、氣孔導度、蒸騰速率、量子產額和羧化效率。黃花杓蘭在天生橋、中甸和昆明的最適光合溫度分別是 18，19 和 21°C，且最適溫度隨光強增加而增加。黃花杓蘭在 3 地的光飽和點為 746-832 $\mu\text{mol m}^{-2}\text{s}^{-1}$ 。黃花杓蘭在低海拔地區光合速率降低主要是因為不能適應高溫，而高溫傷害了其光合機構。結果表明，雖然黃花杓蘭可以在較低海拔地栽培，但需要適宜的農藝措施保證其更好生長，其最適宜的栽培條件是 1/3-1/2 的全光照，氣溫 15-25°C。

關鍵詞：栽培；黃花杓蘭；氣體交換；最適光合溫度；光合能力。