

Characteristics of Gas Exchange in Three Domesticated *Anemone* Species

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ABSTRACT

Seeds of three *Anemone* species were collected from the suburban areas of Kunming and planted in a nursery for three and a half years at Kunming, Yunnan Province, China. Leaf gas exchange measurement indicated that these species had similar one-peak diurnal trends of net photosynthetic rate (P_N), although *A. rivularis* had lower transpiration rate (TR), stomatal conductance (g_s) and intercellular CO_2 concentration (C_i), and higher stomatal limit in the afternoon. Species differences in response of P_N to photosynthetically active radiation (PAR) were observed, especially under strong light. *A. rivularis* had the highest P_N and C_i under strong light which corresponded with its highest g_s and TR. *A. rivularis* had the highest light saturation point (LSP) ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and light compensation point (LCP) ($69 \mu\text{mol m}^{-2} \text{s}^{-1}$), while *A. hupehensis* var. *japonica* had the lowest LSP ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a lower LCP ($53 \mu\text{mol m}^{-2} \text{s}^{-1}$). But the three species responded similarly to the change of CO_2 concentration in the air from 0 to $350 \mu\text{mol (CO}_2\text{) mol}^{-1}$, and their observed CO_2 compensation point showed little difference (47, 53 and $56 \mu\text{mol (CO}_2\text{) mol}^{-1}$). Moreover, *A. rivularis* had the highest apparent quantum yield (0.032), carboxylation efficiency (0.049), P_N ($11.68 \mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$) and TR ($5.36 \text{ mmol (H}_2\text{O) m}^{-2} \text{s}^{-1}$) based on the P_N -PAR response. The results implied that *A. rivularis* is able to grow well under higher radiation, while *A. hupehensis* var. *japonica* is the best one to grow under partial shade.

Keywords: CO_2 Compensation Point, Gas Exchange, Light Compensation Point, Light Saturation Point

1. Introduction

Anemone is a newly developed species for cut flowers that is also used as a potted plant. Many commercial *Anemone* varieties have been released in other countries [1]. *Anemone* is an important genera (25 species, 4 subspecies, and 9 varieties) in Yunnan province, China [2]. Investigations have been reported on taxonomy, cytology and pollen morphology of Anemones [3, 4] and breeding studies were carried out by Hoot [5], Jacob [6] and Lindell [7]. However, photosynthesis has not been documented for the genus.

Many studies are being done on development and utilization of wild flower species for ornamental purpose, of which cultivation of the wild species is one of the important challenges [1]. Three wild *Anemone* species, collected from Yunnan Province, were successfully cultured in a suburban plant nursery at Kunming, but they showed different responses to the light environment. This was reasonable in view of their in situ growth environment, and suggested the importance of controlling light intensity in

artificial culture of these wild plants. Consequently, these *Anemone* species were presumed to have their own peculiarities in photosynthesis. This paper aimed at studying the photosynthetic characteristics of *Anemone* species and their photosynthetic responses to the important components of the environment, providing knowledge for controlling light conditions in the cultivation of *Anemone* species.

2. Materials and Methods

2.1. Plants and Cultivation

Three *Anemone* representative species were selected according to the distribution, leaf and plant form, and growth habit. Seeds were collected from the suburban areas of Kunming, Yunnan Province, China. *A. vitifolia* Buch.-Han. Ex DC. (growing on a stony hillside at 2200 m a.s.l.), *A. rivularis* Buch.-Han. Ex DC. (growing on a grass hillside under sparse trees at 2230m a.s.l.) and *A. hupehensis* Lemoine var. *japonica* (Thunb.) Bowles et Stearn (growing on a limestone wall at 2180 m a.s.l.). Seedlings from

seeds planted in a suburban nursery of light loam soil with satisfied drainage at Kunming in early spring of 2000 (random block design with three replicates, at density of 20×40 cm in 3 m^2 plots). The plants had grown under light shade of trees (50%-100% of natural sunshine, varied along with the angle of incidence), for three and a half years at which time the tests were carried out.

Kunming ($25^{\circ}01'E$, $102^{\circ}41'N$, 1896m a.s.l) has a dry season from November through April and a wet season from May through October, with a yearly mean temperature of 14.9°C , RH of 72%, and an annual rainfall of 1011 mm. The full natural sun radiation at the experimental site was recorded equivalent photosynthetically active radiation $1500\text{--}2000 \mu\text{mol m}^{-2} \text{ s}^{-1}$ on cloud-free days throughout the growth season. The soil prior to the experiment contained 150.3 mg kg^{-1} hydrolysable nitrogen, 25.1 mg kg^{-1} available phosphorus, 250.3 mg kg^{-1} available potassium, 5% of organic matter and with a pH 7.45.

The plants were watered if necessary to avoid water stress during the growing season and were fertilized twice a year before flowering, each time with 80 kg ha^{-1} of urea (46% of N), 100 kg ha^{-1} of normal calcium superphosphate (18% of P_2O_5) and 65 kg ha^{-1} of potassium sulfate (50% of K_2O). The plants showed normal growing, flowering, and fruit setting. The biomass was tested for the species by harvesting all the plots when photosynthesis measurement finished.

2.2. Photosynthesis Measurements and Environmental Data

In late July, 2003 during flower bud stage, net photosyn-

thetic rate (P_N) (3 plants per species, the last fully expanded leaf per plant) in the three species was measured in the field by a portable gas-exchange analyzer (LI-6400, LICOR, Lincoln, NE, USA) (tested leaf area 6cm^2 , air flow rate $400 \mu\text{mol s}^{-1}$, stomatal ratio 0.5, a long tube was used to draw the inlet air far from the operator in order to minimize human impact on the CO_2 levels). Stomatal conductance (g_s), intercellular CO_2 concentration (C_i), transpiration rate (TR), air temperature (T_a), ambient CO_2 concentration (C_a), relative air humidity (RH) and photosynthetically active radiation (PAR) were also recorded.

Diurnal trend of P_N was analyzed at 1-hour intervals from 0700 to 1900 h on a cloud-free day. This was repeated on one subsequent cloud-free day. Leaf water use efficiency (LWUE) was calculated as P_N / TR [8], and stomatal limitation (L_s) as $(C_a - C_i) / C_a$ [9]. The environmental conditions were recorded by the LI-6400 instrument as shown in **Figures 1(a), (b)**. C_a and RH did vary considerably from early morning to nightfall.

The response of photosynthesis to light intensity was measured. P_N was tested from 0830-1130 h on a cloud-free day respectively under PAR 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, and $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (using 6400-02B light source) to set up a response of photosynthesis to light intensity, when T_a , RH, and C_a were $22.5\text{--}28^{\circ}\text{C}$, 45-65%, and $360\text{--}375 \mu\text{mol (CO}_2\text{) mol}^{-1}$. On one subsequent cloud-free day from 0830-1030 h, P_N was tested respectively under PAR 800, 600, 400, 200, 80, 40, and $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ to determine accurate light compensation points in different species, when T_a , RH, and C_a were $23\text{--}26.5^{\circ}\text{C}$, 50-65%, and $365\text{--}375 \mu\text{mol}$

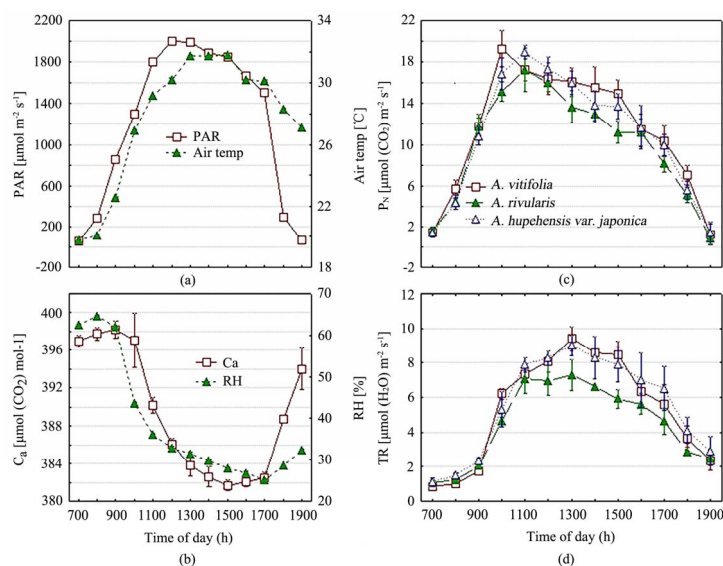


Figure 1. Diurnal trends of the photosynthetically active radiation (PAR), air temperature (T_a), ambient CO_2 concentration (C_a), relative humidity (RH), net photosynthetic rate (P_N) and transpiration rate (TR) in the domesticated *Anemone* species. The symbols and the vertical bars in the figure were mean \pm standard deviation.

(CO₂) mol⁻¹. Sample leaves were first exposed to the highest PAR. When a constant P_N was achieved PAR was lowered step by step to total darkness. At each step, a constant P_N was achieved prior to recording the data. The apparent quantum yield (AQY) was calculated as the initial slope of the regression P_N on PAR under conditions of PAR 0, 40 and 80 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [10-12].

Light saturation points (LSP) were the turning point areas on the curves in **Figure 3(a)**, while light compensation points (LCP) were derived from the linear correlation of P_N and PAR when $\text{PAR} \leq 80 \mu\text{mol m}^{-2} \text{s}^{-1}$ (**Figure 4**), here the constant dependent X (PAR) was considered as LCP, *i.e.*, the PAR value when $P_N = \text{zero}$. CO₂ compensation points (CCP) was determined by the linear correlation between P_N and C_a when $C_a \leq 100 \mu\text{mol (CO}_2\text{) mol}^{-1}$ (**Figure 5(a)**), here the constant dependent X (CO₂) was considered as CCP, *i.e.*, the CO₂ value when $P_N = \text{zero}$.

The response of photosynthesis to CO₂ concentration was measured from 0900-1100 h on another cloud-free day, when T_a and RH were 24-27°C and 55-65%. PAR was set at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ based on the P_N -PAR response (see **Figure 3(a)**), and C_a was set at 0, 50, 100, 150, 200, 250, 300, and 350 $\mu\text{mol (CO}_2\text{) mol}^{-1}$ by adjusting the instrument. The carboxylation efficiency (CE) was calculated as the initial slope of the regression P_N on C_i under conditions of C_a 0, 50 and 100 $\mu\text{mol (CO}_2\text{) mol}^{-1}$ [9,13].

2.3. Data Analysis

P_N and TR values at the seven PAR settings *i.e.* 800, 1000,

1200, 1400, 1600, 1800 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were used for comparing P_N and TR among species. Specific difference was determined by LSD test (Fisher) at $\alpha = 0.05$. Post hoc comparisons for the data in Table 1 and all diagrams were carried out using Statistica 5.0 (StatSoft Inc. (1995) STATISTICA). The vertical bars in the figures were means \pm standard deviations (SD).

3. Results

3.1. Diurnal Patterns of P_N and the Related Parameters

The three species had similar one-peak diurnal trends of P_N showing an asymmetric parabola-like curve (**Figure 1(c)**). *A. vitifolia* had a maximum P_N at 1000 h, the other two at 1100 h. At 1000, 1300-1500 and 1700-1800 h, *A. rivularis* had lower P_N values than *A. vitifolia*. TR showed the same trend peaking at 1300 h (**Figure 1(d)**), but *A. rivularis* had lower TR than the other two from 1200-1700 h.

The diurnal trends of g_s in the three species were similar, but species differences could be seen from the height of peaks and curves, as well as the timing of peak value (**Figure 2(a)**). C_i decreased up to 1000 h and increased after 1700 h (**Figure 2(b)**), showing little change from 1000 to 1700 h at about 280 $\mu\text{mol (CO}_2\text{) mol}^{-1}$, with *A. rivularis* being exceptionally low, the result from the lower values of g_s (**Figure 2(a)**).

LWUE peaked at 0900 h, decreasing from 0900 h to 1100 h due to TR increase (**Figure 1(d)**), then remaining

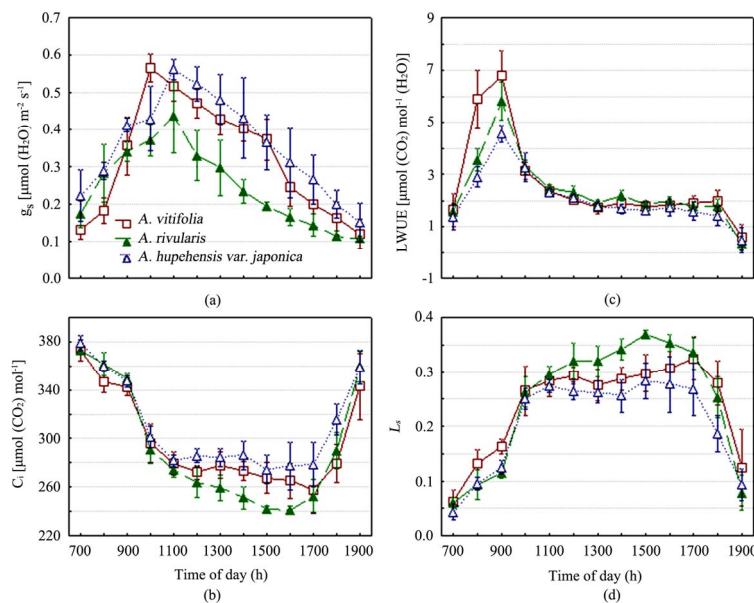


Figure 2. Diurnal trends of the stomatal conductance (g_s), intercellular CO₂ concentration (C_i), leaf water use efficiency (LWUE, = P_N / TR) and stomatal limitation (L_s , = $(C_a - C_i) / C_a$) in the domesticated *Anemone* species. The symbols and the vertical bars in the figure were mean \pm standard deviation.

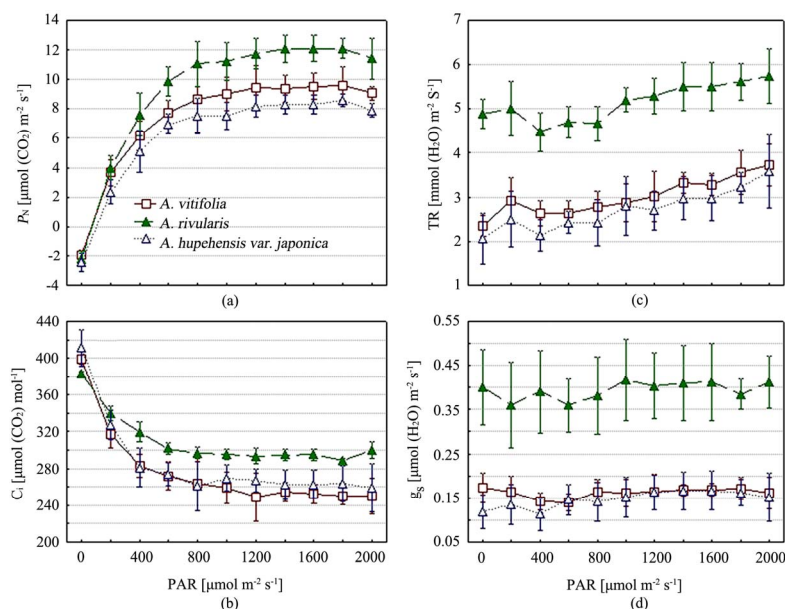


Figure 3. Responses of the net photosynthetic rate (P_N), intercellular CO_2 concentration (C_i), transpiration rate (TR) and stomatal conductance (g_s) to photosynthetically active radiation (PAR) in the domesticated *Anemone* species. The symbols and the vertical bars in the figure were mean \pm standard deviation.

constant until 1800 h (**Figure 2(c)**). L_s showed diurnal variations and all the species maintained high L_s values from 1000 h to 1700 h (**Figure 2(d)**), but *A. rivularis* had the highest values of L_s from 1200 – 1600 h.

3.2. Response of Photosynthesis to Light Intensity

P_N responses to PAR of the considered species showed significant differences under the light intensity of 400 through to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Under this condition, *A. rivularis* had the highest P_N , and *A. hupehensis var. japonica* had the lowest, showing their difference in sensitivity to light intensity (**Figure 3(a)**). P_N increased rapidly when PAR increased from zero to 600 or 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$, although light depression of photosynthesis was not observed within the short time (0900-1100 h) when PAR did not exceed 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$. LSPs were 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *A. rivularis* and *A. vitifolia*, and 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *A. hupehensis var. japonica* (**Figure 3(a)**). LCPs of *A. vitifolia*, *A. hupehensis var. japonica* and *A. rivularis* were 47 ± 1.2 (SD), 53 ± 1.4 and 69 ± 1.6 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (**Figure 4**).

C_i responded to light intensity reversal to P_N (**Figure 3(b)**) and reached 380-410 $\mu\text{mol (CO}_2\text{) mol}^{-1}$ when the leaf was put in dark (PAR = 0). *A. rivularis* had higher C_i values than the other two under light intensity of 200-2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Correlation analysis showed a significantly negative correlation between P_N and C_i ($r = -0.93^*$, data not shown). Moreover, Anemones showed a

stable TR that was influenced little by the increasing PAR (**Figure 3(c)**), and *A. rivularis* had the highest TR values that corresponded with g_s (**Figure 3(d)**).

3.3. Response of Photosynthesis to CO_2 Concentration

To estimate CCP and CE, P_N responses of the *Anemone* species were measured under a range of C_a from 0 to 350 $\mu\text{mol (CO}_2\text{) mol}^{-1}$. P_N increased when C_a increased from

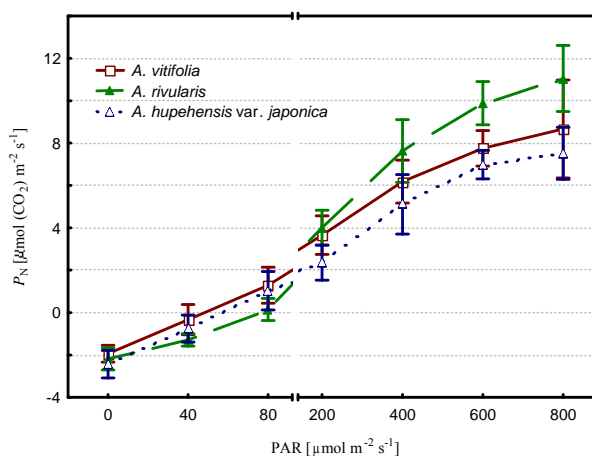


Figure 4. Photosynthetic rate (P_N) of the *Anemone* species under low photosynthetically active radiation (PAR) showing the light compensation point. The symbols and the vertical bars in the figure were mean \pm standard deviation.

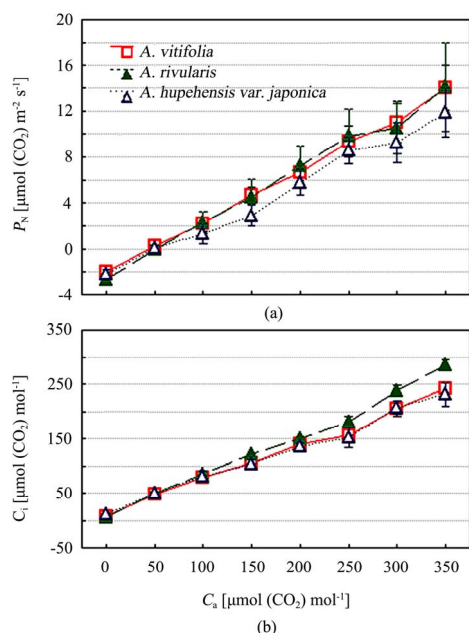


Figure 5. Responses of the net photosynthetic rate (P_N) and intercellular CO₂ concentration (C_i) to ambient CO₂ concentration (C_a) in the domesticated *Anemone* species. The symbols and the vertical bars in the figure were mean \pm standard deviation.

0 to 350 $\mu\text{mol (CO}_2\text{) mol}^{-1}$, showing insignificant differences among the considered species (**Figure 5(a)**). C_i showed same response to the change of C_a (**Figure 5(b)**). CCP was 47 ± 1.0 (SD) $\mu\text{mol (CO}_2\text{) mol}^{-1}$ for *A. vitifolia*, 53 ± 1.1 for *A. rivularis* and 56 ± 1.4 for *A. hupehensis* var. *japonica* (**Figure 5(a)**).

3.4. Differences in P_N , TR, CE, AQY and Biomass

P_N and TR were compared according to the data of P_N /TR-PAR responses within PAR 800-2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and showed significant specific difference (**Table 1**). *A. rivularis* had the highest P_N and TR, while *A. hupehensis* var. *japonica* had the lowest. The specific difference was observed in biomass that showed a close correlation with

P_N ($r = 0.991^*$, **Table 1**).

CE varied from 0.036 to 0.049 among the species with *A. rivularis* having the highest CE. The specific difference in CE showed a close correlation with P_N values ($r = 0.999^*$, **Table 1**). AQY was in the range 0.023 to 0.032; *A. rivularis* again had the highest value. AQY was also closely associated with P_N values ($r = 0.999^*$, **Table 1**).

4. Discussion

4.1. Diurnal Trend of Photosynthetic Rate

In this experiment, the major environmental factors, PAR, T_a and air RH changed remarkably during the day as shown in **Figures 1(a), (b)**. This situation is normal at our experimental site and is the driver of P_N daily change. No increase of P_N was observed in the afternoon while a midday depression in photosynthesis was found in *Anemone* species collected from the alpine region in suburban areas of Kunming (1896 m a.s.l.). P_N increased before 1000 or 1100 h and decreased from 1000 or 1100 h (dependent on species) onwards. The increase of P_N in the morning was driven by the increase of PAR and g_s (**Figures 1(a), (c)**; **Figure 2(a)**), and decrease of P_N from the late morning to the afternoon was caused by the decrease of g_s (**Figure 1(c)**; **Figure 2(a)**). A close link between P_N and g_s and/or PAR (only in the morning) was observed in the investigation of the diurnal trends of photosynthetic rate for *Ginkgo biloba*, *Paspalum notatum*, and *Enkleia malaccensis* [14-16]. Whereas g_s decrease in this experiment resulted from the integrative action of adverse ecological factors such as the rise of T_a ($> 30^\circ\text{C}$), decrease of air RH ($< 35\%$) and C_a ($< 386 \mu\text{mol (CO}_2\text{) mol}^{-1}$), and strong light ($> 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$) (**Figures 1(a), (b)**). A strong light of no more than $1800 \mu\text{mol m}^{-2} \text{s}^{-1}$ did not depress the photosynthesis of the Anemones in the field (**Figure 3(a)**). This may reflect the intrinsic adaptation of the *Anemone* species to the mild ecological environments in their native habitats of moderate T_a , higher air RH but strong light. The decrease of g_s from 1000 or 1100 h onwards and the decrease of TR in the afternoon were caused by the increase of stomatal limitation (L_s)

Table 1. Carboxylation efficiency (CE), apparent quantum yield (AQY), Photosynthetic rate (P_N), transpiration rate (TR) and biomass of the *Anemone* species.

Taxon	CE	AQY	P_N	TR	Biomass (kg m ⁻²)
<i>A. rivularis</i>	0.0491 ± 0.0014^a	0.0317 ± 0.0005^a	11.68 ± 0.448^a	5.36 ± 0.354^a	1.02 ± 0.055^a
<i>A. vitifolia</i>	0.0417 ± 0.0011^b	0.0275 ± 0.0007^b	9.25 ± 0.346^b	3.22 ± 0.351^b	0.83 ± 0.071^b
<i>A. hupehensis</i> var. <i>japonica</i>	0.0355 ± 0.0013^c	0.0229 ± 0.0009^c	8.05 ± 0.420^c	2.96 ± 0.372^b	0.78 ± 0.069^b

P_N and TR values at the seven PAR settings *i.e.* 800, 1000, 1200, 1400, 1600, 1800 and 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were used for comparing P_N and TR among species. Numbers in the table are means \pm SD. Same letters show no statistical difference among species by LSD test (Fisher) at $\alpha = 0.05$. Correlation coefficients of P_N -AQY and P_N -Biomass were 0.999* and 0.991*.

(Figure 1(d); Figures 2(a), (d)). Here TR seemed to have a delayed response to the change of L_s , but in fact TR was tightly linked to the increasing T_a , PAR and vapor pressure deficit based on leaf temperature (VpdL), and decreasing RH (Correlation coefficients of TR with PAR, T_a , VpdL and RH were derived as 0.89*, 0.86*, 0.61* and -0.72*, respectively) (data not shown). This led to a high level of TR around noon even though at this time g_s decreased and/or L_s increased. Therefore, PAR, T_a and RH were the major drivers of TR (Figures 1(a), (b) and (d)), as VpdL negatively correlated with RH ($r = -0.94^*$) (data not shown).

The decrease of C_i is the major criterion for verifying L_s if P_N decreased or stayed at a low level [17]. In our experiment, C_i obviously decreased in the morning before 1100 h that reflected the normal changes from night (where C_i increased over time because of respiration) to daytime from increased intercellular CO_2 use resulting from increasing photosynthesis. The decrease of C_i in *A. rivularis* from 1100 h until 1600 h (Figure 2(b)) was likely caused by the decrease of g_s (Figure 2(a)) since P_N decreased as well during this period (Figure 1(c)) and water stress was avoided by watering. Based on the above argument, the decrease of P_N from the late morning to the afternoon was mainly caused by a shortage of CO_2 resulted from an increase of L_s and decrease of g_s (Figure 1(c); Figures 2(a), (d)). It is well known that the increase of C_i is the reason for non-stomatal limitation of photosynthesis when P_N is at a low level [18]. Therefore, the rapid decrease of P_N after 1700 h was caused by an increase of non-stomatal limitation (e.g., carboxylation resistance) that quite likely resulted from the decrease of PAR (Figure 1(a)), for even if g_s was at a low level, C_i increased and L_s decreased rapidly during this time. There is a strong correlation between P_N and g_s because stomata respond to the changes in assimilation via C_i . Correlation analysis revealed a significantly positive correlation between P_N and g_s ($r = 0.77^*$), and a negative correlation between P_N and C_i ($r = -0.73^*$) (data not shown).

When PAR was set to zero, the P_N values of -2.5 – -2.0 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$ might reflected the respiration rates of the Anemones under the experimental conditions (Figure 4).

4.2. Response of Photosynthesis to Light Intensity

In lettuce [19], tobacco [20], and *Phaseolus vulgaris* [21], P_N along with the increase of light intensity increased to a peak, then decreased if the light intensity increased further. However, in ramie (*Boehmeria nivea* (L.) Gaud.) [22], tomato [23], cucumber [17], and cotton [24], as light intensity increased, P_N increased and kept on at a high

level within a wide range of light intensity. The depression of photosynthesis in tobacco when PAR > 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was due to the reduction in activities of PSI and PSII, carbonic anhydrase and electron transfer speed [20]. A large decrease in stomatal conductance to water vapour in *Phaseolus vulgaris* leaves exposed to strong light was found [21].

In our experiments, strong light of no more than PAR 1800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ did not depress photosynthesis, although differences were observed in utilization of light energy under high light intensity (Figure 3(a)) with adequate soil water, T_a 23–30°C and RH 45–65%. Furthermore, the sample leaf was put under a strong light for a few minutes for achieving a constant P_N before going to a lower PAR. Therefore, it needs more investigations to uncover whether or not the *Anemone* species have a photosystem insensitive to the change of light intensity. The experiment results, based on single leaf test, suggested that PAR 800–1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ is enough for a satisfactory P_N and meets the needs for photosynthetic products for normal growth and development of *Anemone* cultivation.

Among the three species, *A. rivularis* was from a grass hillside under sparse trees with good sunshine and had a different response to light from other species, showing a high LCP and LSP. Whereas, *A. hupehensis* var. *japonica* was from a limestone wall with only intermittent sunshine and is probably less well adapted to continuous strong light. The light response data, low LCP and LSP, and low maximum P_N value all indicated that this species is the best one to grow under partial shade.

4.3. Response of Photosynthesis to CO_2

Among P_N , TR, g_s , and C_i , only P_N and C_i were observed to increase regularly as C_a increased, and the response of P_N and C_i to the change of C_a showed little difference among the species (Figures 5(a), (b)). When C_a was set to zero, P_N was -3 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$ (Figure 5(a)) which was roughly considered as the sum of respiration and photorespiration under the experimental conditions. This was unlike the P_N values at PAR = 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ where the minus P_N values just presented the respiration rates. The CO_2 saturation curve of photosynthesis in the considered species is still in need of study.

A higher CCP (60–75 $\mu\text{mol (CO}_2\text{) mol}^{-1}$), but a much lower LCP (13–28 $\mu\text{mol m}^{-2} \text{s}^{-1}$), and similar diurnal curves of P_N and TR were observed in domesticated *Primula* species collected from an alpine area of north-western Yunnan Province, China [25]. This reflected the similarity in photosynthetic daily patterns of Anemones and Primulas as alpine plants, and the dissimilarity in light and CO_2 utilization qualities of plants of the two genera, which should be taken into consideration for their cultivation.

5. Conclusions

The *Anemone* species described here showed similar one-peak diurnal trends of P_N , although *A. rivularis* had lower TR, g_s , and C_i , and higher L_s in the afternoon. Specific differences in response of P_N to PAR were observed, especially under strong light. *A. rivularis* had the highest P_N and C_i under strong light which corresponded with its high g_s and TR. *A. rivularis* had the highest LSP ($1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and LCP ($69 \mu\text{mol m}^{-2} \text{s}^{-1}$), while *A. hupehensis* var. *japonica* had the lowest LSP ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) and a lower LCP ($53 \mu\text{mol m}^{-2} \text{s}^{-1}$). All these species responded similarly to the change of C_a from 0 to $350 \mu\text{mol} (\text{CO}_2) \text{mol}^{-1}$, and their CCP showed little difference. Moreover, *A. rivularis* had the highest AQY, CE, P_N and TR based on the P_N -PAR response. In conclusion, *A. rivularis* is able to grow well under higher radiation, while *A. hupehensis* var. *japonica* is the best one to grow under partial shade.

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