

Photosynthetic responses of apricot (*Prunus armeniaca* L.) to photosynthetic photon flux density, leaf temperature, and CO₂ concentration

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Abstract

Two cultivars (Katy and Erhuacao) of apricot (*Prunus armeniaca* L.) were evaluated under open-field and solar-heated greenhouse conditions in northwest China, to determine the effect of photosynthetic photon flux density (PPFD), leaf temperature, and CO₂ concentration on the net photosynthetic rate (P_N). In greenhouse, Katy registered 28.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for compensation irradiance and 823 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for saturation irradiance, which were 73 and 117 % of those required by Erhuacao, respectively. The optimum temperatures for cvs. Katy and Erhuacao were 25 and 35 °C in open-field and 22 and 30 °C in greenhouse, respectively. At optimal temperatures, P_N of the field-grown Katy was 16.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 21 % less than for a greenhouse-grown apricot. Both cultivars responded positively to CO₂ concentrations below the CO₂ saturation concentration, whereas Katy exhibited greater P_N (18 %) and higher carboxylation efficiency (91 %) than Erhuacao at optimal CO₂ concentration. Both cultivars exhibited greater photosynthesis in solar-heated greenhouses than in open-field, but Katy performed better than Erhuacao under greenhouse conditions.

Additional key words: acclimation; compensation and saturation values; intercellular CO₂ concentration; net photosynthetic rate; saturation irradiance; stomatal conductance; transpiration rate.

Introduction

Apricot is one of the most important and profitable fruit trees in northwest China. In the greenhouse, apricot fruits mature at least 50 d earlier than those grown under open-field conditions. As demand for year-around fresh fruit has increased, the price of apricot fruits produced in the greenhouse is 4 times higher than in the open-field growth. In the recent years, the production of apricot fruits in solar-heated (heated only by the sun) plastic-covered greenhouses [lower photosynthetic photon flux density (PPFD), fluctuant CO₂ concentration and temperature are the main differences compared with field] has markedly increased. The photosynthetic process is an integral part of plant growth and development, with the carbon assimilates necessary for yield production ultimately produced *via* photosynthesis. Thus, the alteration of the net photosynthetic rate (P_N) can influence plant growth.

Apricot performs well under climate of long day and high irradiance. Low PPFD is the major factor limiting greenhouse apricot fruit production (Wang *et al.* 2000). Under these conditions, the plant often acclimates to irradiance, and this acclimation promotes plant growth and fruit development. Similar observations have been reported on other crops such as peach (nectarine) (Wang *et al.* 2000), pepper (Wang *et al.* 1999), and cucumber (Ma and Pang 1997). Also, the dynamics of CO₂ in solar-heated greenhouses differs from that in open-field (Yu *et al.* 1998). In greenhouses, the CO₂ concentration changes dramatically during the day (Table 1). Constant high CO₂ can result in photosynthetic acclimation (Osborne *et al.* 1998, Rogers *et al.* 1998, Tischler *et al.* 2000), but the effect of the varying CO₂ during the day on the photosynthetic property of apricot is still unknown.

Received 27 July 2005, accepted 30 June 2006.

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Abbreviations: AQY = apparent quantum yield; CE = carboxylation efficiency; C_i = intercellular CO₂ concentration; CI = compensation irradiance; P_N = net photosynthetic rate; PPFD = photosynthetic photon flux density; RuBP_{max} = maximum regeneration rate of ribulose-1,5-bisphosphate; R^2 = determination coefficient; SCC = saturation CO₂ concentration; SI = saturation irradiance; Γ = CO₂ compensation concentration.

Acknowledgements: This study was funded by the State Key Laboratory of Arid Agroecology of Lanzhou University, Gansu, China. We also gratefully acknowledge Dr. Lu Jiang for providing critical review to the manuscript.

Table 1. Diurnal variations of main ecological factors and their effects on net photosynthetic rate (P_N), transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (C_i) of apricot cv. Katy in greenhouse, 30 d after blossom.

Time	CO_2 ref. [$\mu mol\ mol^{-1}$]	PPFD [$\mu mol\ m^{-2}\ s^{-1}$]	Air temp. [$^{\circ}C$]	E [$mmol\ m^{-2}\ s^{-1}$]	g_s [$mmol\ m^{-2}\ s^{-1}$]	Leaf temp. [$^{\circ}C$]	C_i [$\mu mol\ mol^{-1}$]	P_N [$\mu mol\ m^{-2}\ s^{-1}$]	Mb ref.
09:00	858.7	98	19.2	1.73	190	18.5	747	9.1	10.7
10:00	671.3	157	26.9	2.06	165	26.2	606	4.1	20.1
11:00	424.6	476	28.9	4.39	265	27.7	293	14.5	15.0
12:00	392.4	707	26.5	4.37	289	25.6	248	17.4	12.3
13:00	396.3	765	26.1	4.61	325	24.8	270	16.3	11.6
14:00	393.7	883	26.9	4.78	278	26.1	263	14.9	10.6
15:00	400.0	520	21.1	3.44	272	20.3	266	15.4	7.2
16:00	377.9	230	31.2	6.93	346	28.6	301	8.9	10.5
17:00	460.8	21	22.9	1.34	67	22.3	386	2.3	7.8

Additionally, CO_2 enrichment has been widely used in China for greenhouse fruit production, but the photosynthetic response of apricot to enriched CO_2 has not been studied intensively.

In recent years, photosynthesis of fruit trees has been studied in banana (Thomas and Turner 2001), mango (Shivashankara and Mathai 2000), grape (Patakas *et al.* 2003, Cohen *et al.* 2005), apple (Jia and Li 2002, Mierowska *et al.* 2002), almond (De Herralde *et al.* 2003, Matos *et al.* 2004), jujube (Su and Liu 2005), *etc.* But no

research has been reported on apricot acclimation in controlled environments. Little information is available on the responses of photosynthesis to solar heated greenhouse conditions in woody plants including apricot. Therefore, the objective of this research was to determine: (1) whether differences in the photosynthetic response to different growth conditions and different apricot genotypes exist, and (2) whether the studied cultivars acclimate to the greenhouse growth conditions.

Materials and methods

Plants and growth conditions: Two sets of experiments were conducted with plants grown either in greenhouse or in the field. The field experiment was conducted in Lanzhou city of Gansu province, located at $36^{\circ}03'N$, $104^{\circ}38'E$, and 1 530 m a.s.l. The climate is continental monsoon type with a severe and dry winter, high temperatures, and concentrated rainfalls in the summer. Annual sunshine is around 2 650 h, annual average available accumulated temperature ($\geq 10^{\circ}C$) is 3 242 $^{\circ}C$, and there are 195 frost-free days in a normal year. The plants were planted in April 2001 with a designed population of 825 plants per ha. Row space was 4 m. Conventional farming techniques were used.

The greenhouse experiment was conducted in Baiyin city of Gansu province, 70 km north of Lanzhou. Three-year-old seedlings were transplanted into 1 500 cm^3 containers filled with a mixture of sand, organic fertilizer, and soil (1 : 2 : 6, v/v/v) on 2 April, 2003. On 9 November, 2003, the containers were placed into the greenhouse at a depth of 40 cm and a designed plant population of 6 660 plants per ha, seven times higher than that used in the field experiment. Special techniques for apricot grown in greenhouses were used. Two cultivars, Erhuacao and Katy, were used for greenhouse and open-field experiments, 30 d after blossom in 2004.

Gas exchange: A portable photosynthesis system (model CIRAS-1, PP-System, UK) was used to measure P_N of the

tagged leaves. The system was equipped with an automatic cuvette and was set up to adjust airflow so that vapour pressure deficit and relative humidity remained constant during measurements. A 12-V mobile battery was connected to the system to supply the necessary power requirements. Treatments consisted of three variables: (a) PPFD that was changed from high to low in the range of 2 000 to 0 $\mu mol\ m^{-2}\ s^{-1}$, (b) the CO_2 concentration was changed from low to high in the range of 0 to 2 000 $\mu mol\ mol^{-1}$, and (c) air temperature ranged between 5 and 45 $^{\circ}C$. Among the three variables, when one variable was changed (by adjusting and controlling the PP-system) as designed for the treatments, the other two remained constant. For example, when determining the photosynthetic responses to PPFD changing from 0 to 2 000 $\mu mol\ m^{-2}\ s^{-1}$, air temperature remained at 25 $^{\circ}C$, and CO_2 concentration remained at 400 $\mu mol\ mol^{-1}$. These constants were based on the recommendations of previous works. The values of stomatal conductance (g_s), intercellular CO_2 concentration (C_i), and transpiration rate (E) were calculated directly from the software of the PP-System that was set up appropriately prior to measurements.

All measurements were conducted between 08:30 and 12:00, 30 d after blossom. The incoming radiation reaching plants was controlled in order to avoid possible impact of assimilate accumulation on P_N . Measurements were repeated to obtain at least four stable readings for

each of the marked leaves.

Experimental design and statistical analysis: Ten uniform sized plants of each cultivar were selected randomly, and two fully expanded, disease-free, fully sunlit leaves were measured on each plant. Namely, 20 leaves were measured totally for each treatment. Three leaves which had the maximal and similar photosynthetic capacity among these 20 leaves on different plants were chosen as three replications per treatment. These three leaves were tagged and used for the following measurements. The tagging process was completed 1–2 d before the formal measurements.

The data recorded in the PP-system were transferred directly to a computer for statistical analyses. Data measured from the tagged leaves were averaged to simplify the analyses. These equation-generated parameters were used to describe quantitatively the photosynthetic responses. For example, the parameters of compen-

Results

PPFD- P_N : Under open-field conditions, the cv. Katy responded to PPFD in a pattern similar to that of cv. Erhuacao. Initially, P_N increased with PPFD before SI, and then the P_N was stabilized for both cultivars (Fig. 1A,B). Under greenhouse condition, Katy registered 28.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for CI, it is about 73 % as much as required by Erhuacao. Otherwise, cv. Katy registered 823 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for SI, it is 118 % as much as required by cv. Erhuacao. Katy produced a greater AQY than Erhuacao. As PPFD approached the LSP, Katy and Erhuacao produced greatly different P_N , respectively (22.37 and 16.12 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Table 2).

The apricot Erhuacao grown in the solar-heated greenhouse produced a similar PPFD response pattern as those grown under open-field condition (Fig. 1A). With the increase of PPFD, the P_N increased rapidly before PPFD approached ca. 600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and then was stabilized. Compared to open-field, Erhuacao grown in the greenhouse had higher CI and SI, but produced similar AQY and P_N values (Fig. 1A and Table 2).

Cv. Katy grown in solar-heated greenhouse also produced a similar PPFD response pattern as plants grown under open-field condition. Compared to open-field, it had higher CI and SI values, and produced 33 % higher AQY in greenhouse (Table 2). At SI, the P_N of cv. Katy grown in greenhouse was 22.37 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is 39 % higher than obtained in open-field.

Temperature response: Temperature had a great effect on the P_N of apricot under both growth conditions. P_N increased with leaf temperature and then decreased. Large differences in the response were found between the two growth environments, in cv. Katy the P_N was significantly greater for plant grown in the greenhouse than in the open-field (20.9 and 16.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively)

sation irradiance (CI), saturation irradiance (SI), and apparent quantum yield (AQY) were generated from evaluating the equations of the P_N response to PPFD. The values of these parameters were obtained from the first derivatives of the equations. The AQY was defined as the slope of the regression curve at $\text{PPFD} \leq 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Zou *et al.* 1994, An *et al.* 1998). Similarly, the parameters of CO₂ compensation concentration (CCC) and CO₂ saturation concentration (CSC) were obtained from the derivations of the equation that was developed to describe the P_N response to CO₂ concentration. The maximum RuBP regenerating rate (RuBP_{max}) was defined as the P_N at CSC (Zou *et al.* 1994, An *et al.* 1998). The carboxylation efficiency (CE) was determined as the slope of the response curves at CO₂ concentration $\leq 300 \mu\text{mol mol}^{-1}$ (Zou *et al.* 1994). Standard error (SE) was calculated and differences in mean values for each treatment were tested at $p < 0.05$ according to the test of least significant difference (LSD).

at their optimal temperatures (22 and 35 °C, respectively; Fig. 2). But for Erhuacao, there were no significant differences between plants grown in both environments, although their optimal temperatures were also around 25 and 30 °C, respectively (Fig. 2).

In the greenhouse, cv. Katy also had higher P_N value (20.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$) than cv. Erhuacao (14.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$)

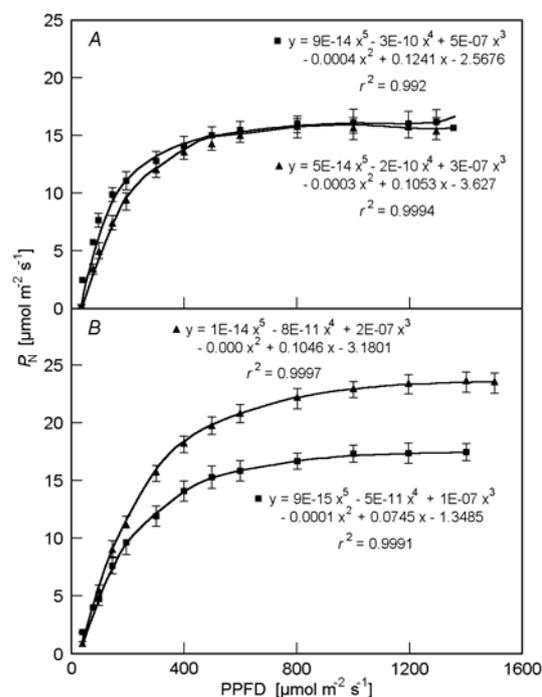


Fig. 1. Net photosynthetic responses (P_N) of apricot to photosynthetic photon flux density (PPFD) of cvs. Erhuacao (A) and Katy (B), when grown under open-field (■) and solar-heated greenhouse (▲) in northwest China. Means \pm SE.

Table 2. Compensation irradiance (CI), saturation irradiance (SI), apparent quantum yield index (AQY), net photosynthetic rate (P_N) at SI, CO₂ compensation concentration (Γ), saturation CO₂ concentration (SCC), carboxylation efficiency (CE), and the maximum regeneration rate of ribulose-1,5-bisphosphate (RuBP_{max}) for two apricot cultivars (Erh = Erhuacao) grown under open-field (OF) and greenhouse (G) conditions in northwest China. Means \pm SE that do not share the same letter for a certain parameter were significantly different ($p < 0.01$).

Cultivar, growth	CI [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	SI [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	AQY	P_N at SI [$\mu\text{mol m}^{-2} \text{s}^{-1}$]	Γ [$\mu\text{mol mol}^{-1}$]	SCC [$\mu\text{mol mol}^{-1}$]	CE	RuBP _{max} [$\mu\text{mol m}^{-2} \text{s}^{-1}$]
Erh, OF	12.0 \pm 1.8 C	550 \pm 12.2 D	0.053 \pm 0.012 B	15.56 \pm 3.21 B	65.0 \pm 5.2 C	1350 \pm 23 AB	0.052 \pm 0.021 C	28.0 \pm 3.6 B
Katy, OF	10.1 \pm 2.0C	604 \pm 20.3 C	0.050 \pm 0.010 B	16.10 \pm 1.62 B	78.3 \pm 4.3 B	1250 \pm 31 B	0.071 \pm 0.019 A	33.5 \pm 3.4 A
Erh, G	38.7 \pm 1.7A	698 \pm 16.3 B	0.056 \pm 0.009 B	16.12 \pm 3.25 B	90.8 \pm 2.6 A	1450 \pm 53 A	0.033 \pm 0.011 D	43.3 \pm 5.9 B
Katy, G	28.3 \pm 3.2B	823 \pm 23.1 A	0.066 \pm 0.020 A	22.37 \pm 2.68 A	65.2 \pm 3.5 C	1400 \pm 21 AB	0.064 \pm 0.016 B	51.1 \pm 4.6 A

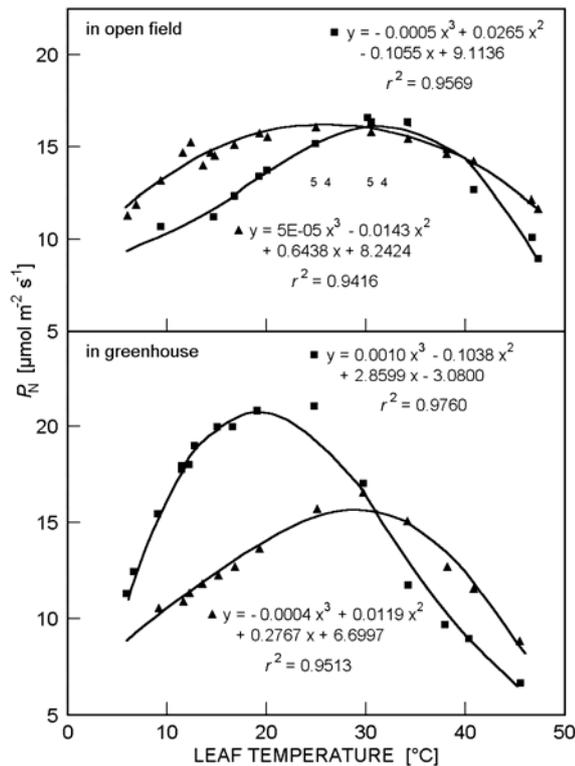


Fig. 2. Net photosynthetic responses (P_N) to leaf temperatures of apricot cultivars Erhuacao (▲) and Katy (■) when grown under open-field and in solar-heated greenhouse.

at optimal temperatures (22 and 30 °C, respectively). But in the open-field, the two cultivars had similar peak P_N values at their optimal temperatures of 25 and 35 °C, respectively (Fig. 2).

With the leaf temperature increase of greenhouse-grown Katy, g_s increased rapidly, peaked around 15 °C, and then decreased sharply (Fig. 3A). This pattern was somewhat similar to the pattern of P_N response to leaf temperature (Fig. 2), where the peak of the P_N response occurred at a temperature around 20–25 °C. Furthermore, as leaf temperature increased, E increased steadily (Fig. 3A), while C_i decreased rapidly before the leaf temperature reached around 30 °C, and then increased (Fig. 3B).

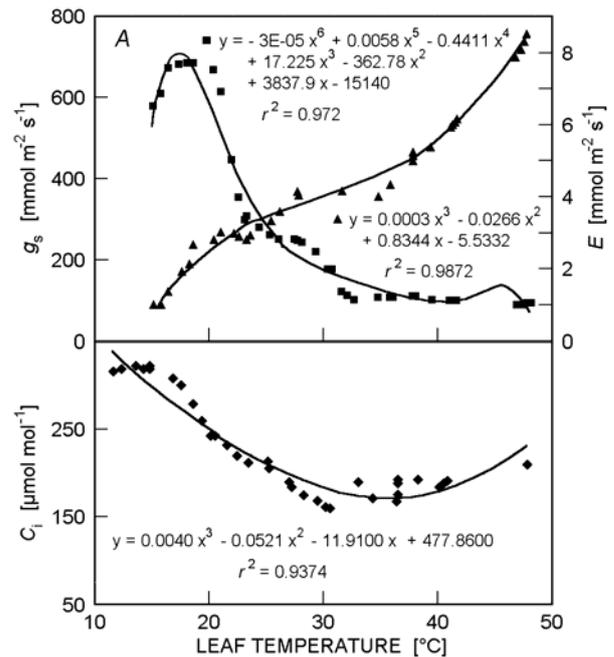


Fig. 3. Relationships between leaf temperature and stomatal conductance, g_s (■), transpiration rate, E (▲), and intercellular CO₂ concentration, C_i (◆) for the apricot cv. Katy grown under a solar-heated greenhouse in northwest China.

P_N - C_i curves: Although the two cultivars have a different genetic background, they had similar response patterns to CO₂ concentration at low CO₂ concentration, however, the two cultivars differed in the magnitude of response (Fig. 4). The increment of the P_N response curve was steeper for Katy than for Erhuacao when CO₂ was ≤ 1 200 $\mu\text{mol mol}^{-1}$ in open-field (≤ 1 000 $\mu\text{mol mol}^{-1}$ in greenhouse), indicating that Katy responded to CO₂ concentration more strongly than Erhuacao. Additionally, the values of Γ , CE, SCC, and RuBP_{max} were significantly different between the two cultivars when grown in the greenhouse. Cv. Katy had a lower CC value than cv. Erhuacao, otherwise, both SCC values were similar. However, Katy produced higher CE (91 %) and RuBP_{max} (18 %) than Erhuacao (Table 2). But in the open-field, both had lower CCC, SCC, and RuBP_{max}, and a higher CE than when grown in the greenhouse.

Discussion

The response of plant to variable and stressful environments has been studied for a long time because it limits the distribution and productivity. In our study, the irradiance in the greenhouse was lower than in the open field. Photosynthetic activity of Katy was significantly increased in greenhouse, particularly when the CO₂ concentration was above 400 μmol mol⁻¹. The results corroborate the conclusions of earlier investigations (Szente *et al.* 1998, Harnos *et al.* 2002).

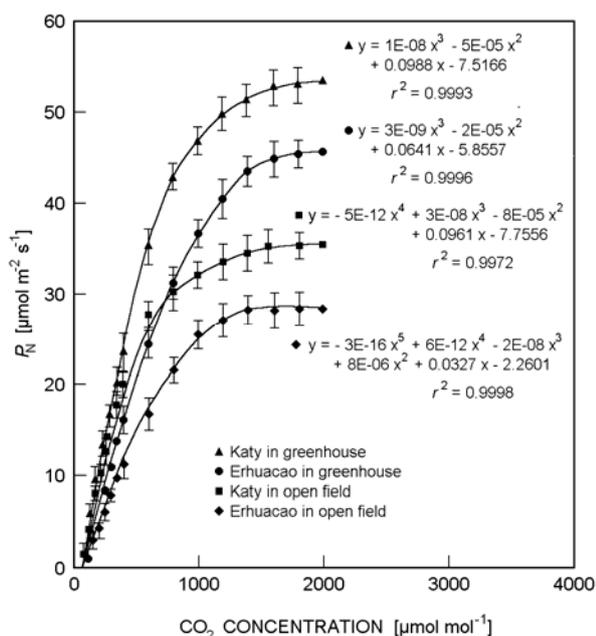


Fig. 4. Photosynthetic response curves of apricot to ambient CO₂ concentration of apricot cultivars Katy and Erhuacao when grown under open-field and greenhouse conditions. Means \pm SE.

The two cultivars differed greatly in response to irradiance (Table 2). Cv. Katy had a lower CI and higher SI compared to cv. Erhuacao, indicating that cv. Katy has a greater P_N than Erhuacao when the PPFD is below SI. Furthermore, in the greenhouse, Katy and Erhuacao produced greatly different P_N (Table 2), indicating that the two cultivars have a different photosynthetic potential when irradiance becomes optimal. Compared with open-field-grown Katy, the higher P_N , AQY, and SI for the greenhouse-grown Katy suggest that Katy grown in a lower PPFD environment could increase its photosynthetic capacity. Our results are similar to those of Wang *et al.* (2000) for greenhouse-grown nectarine (*Prunus*

persica L.), where both cultivars exhibited good adaptation to low irradiance. Wang *et al.* (2000) speculated that the better photosynthetic responses of nectarine to low irradiance might be due to the genetic makeup adaptation history.

Sage *et al.* (1995) reported that an increase in temperature from 25 to 35 °C enhanced photosynthesis by up to 40 % in C₃ plants. This was corroborated by our results except the Katy plant grown in greenhouse, the optimal temperature is around 22 °C. And this was confirmed by the positive response of g_s , leaf E and C_i to leaf temperature.

In greenhouse, CO₂ concentration was higher than outside in the morning because the organic fertilizer released CO₂ as it decomposed. Plant grown under higher CO₂ concentration had an increased P_N and decreased E leading to better water use efficiency (Tuba *et al.* 1996). Also, it was reported that high CO₂ concentration coupled with low irradiance and low temperature in greenhouses reduces transport of the photosynthates (Grodzinski *et al.* 1998), decreases gas exchange (Cao and Sun 1998), and promotes irregular stomatal closure (Peet *et al.* 1986). High CO₂ concentration also decreases the activity of photosynthesis-related enzymes in mesophyll cells, causing CO₂ acclimation in leaves (Yu *et al.* 1998). In our experiment, both cultivars had an increased P_N when grown in the greenhouse as a result of a long-term growth in elevated CO₂ concentration. Cvs. Erhuacao and Katy had similar response patterns to CO₂ concentration at the low CO₂ values. However, the two cultivars differed in the magnitude of response, indicating that Katy responded to CO₂ concentration more sensitively than Erhuacao. Additionally, compared to Erhuacao, Katy had a lower Γ value and a similar SC value, indicating that Erhuacao can use a wider range of CO₂ concentrations for photosynthesis. However, in the greenhouse Katy produced a higher (91 %) CE and higher (18 %) RuBP_{max} than Erhuacao, which suggests that Katy experienced a longer period of CO₂ acclimation; this is a possible reflection of its genetic makeup.

Our present results support that the apricot plants could acclimate to the solar-heated greenhouse condition. However, the acclimation is heavily dependent on the genotype. In comparison with Erhuacao, the cv. Katy has a higher ability to acclimate to the greenhouse condition. The photosynthetic response of apricot to PPFD, CO₂ concentration, and temperature can be used to screen apricot plants with higher acclimation ability grown in the greenhouse.

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