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Full Length Research Paper

Difference in photosynthetic performance among three peach cultivars grown under low light conditions in greenhouses

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The effects of low photosynthetic photon flux density (PPFD) on greenhouse grown peach trees (‘Qingfeng’: *Prunus persica* L. Batsch, ‘NJN76’: *Prunus persica* L. Batsch and ‘Maixiang’: *P. persica* var. nectarine) were investigated. Difference in photosynthesis rate (Pn) and stoma morphology among cultivars were studied. Furthermore, chlorophyll content, leaf thickness and photosynthesis enzyme activity were analyzed. Results showed that when PPFD was reduced to 80% of control, Pn decreased in all three cultivars. The reduced net photosynthesis rate was associated with decreased stoma density, stoma aperture and stoma conductance (Cs), as well as chlorophyll *a* (Chl*a*) and *b* (Chl*b*) content in all cultivars; leaf mass per unit area (LMA) and thickness of upper and lower layers of leaf epidermis also declined. At 80% PPFD, the variation pattern of ribulose bisphosphate carboxylase (RuBPCase), Ca^{2+}-adenosinetriphosphatase (Ca^{2+}-ATPase) and Mg^{2+}- adenosine triphosphatase (Mg^{2+}-ATPase) activities, together with nicotinamide adenine dinucleotide phosphate (NADPH) content and photosynthetic O_2 evolution rate among the three cultivars was the same as the pattern of LMA. Time course analysis showed that the net photosynthesis rate of ‘Maixiang’ was higher than that of the other two cultivars from 10:00 to 14:00. Though the parameters mentioned above decreased under shade in all the three cultivars, ‘Maixiang’ still had higher Pn than that of the other two cultivars. Our results indicated that ‘Maixiang’ is probably more suitable to grow in low PPFD than ‘Qingfeng’ and ‘NJN76’, especially in the early spring season in order to get higher market value.

Key words: *Prunus persica* L., low light, photosynthesis, RuBPcase, Ca^{2+}-ATPase, Mg^{2+}-ATPase, NADPH content.

INTRODUCTION

In China, increasing number of fruit growers are growing peach trees in greenhouses, rather than the open field, for early fruit harvest and better marketing. Commonly, greenhouse grown peach trees are grown in conditions where natural sunlight is the sole source of illumination and there is no additional heating system. In such greenhouses in Beijing 39.92°N, China, peach trees blossom in February and fruit can be harvested in April. During that period, from February to April, the photosynthetic photon flux density (PPFD) is about 200 ~ 300 μmol m^{-2} s^{-1}, and peach trees’ canopies expand and fill up space quickly (Yao et al., 2007). However, many upright and vigorous shoots are produced on the trees, resulting in shading, especially of the low layers of peach tree canopies; and when combined with the poor light condition inside the greenhouse, the productivity of the peach trees is markedly reduced.

It is well known that plant growth and development is significantly affected by environmental factors. If plants

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Abbreviations: PPFD, Photosynthetic photon flux density; **RuBPCase**, bisphosphate carboxylase**; LMA**, leaf mass per unit area; **Ca^{2+}-ATPase**, Ca^{2+}-adenosinetriphosphatase**; Mg^{2+}-ATPase**, Mg^{2+}-adenosine triphosphatase**; NADPH**, nicotinamide adenine dinucleotide phosphate.

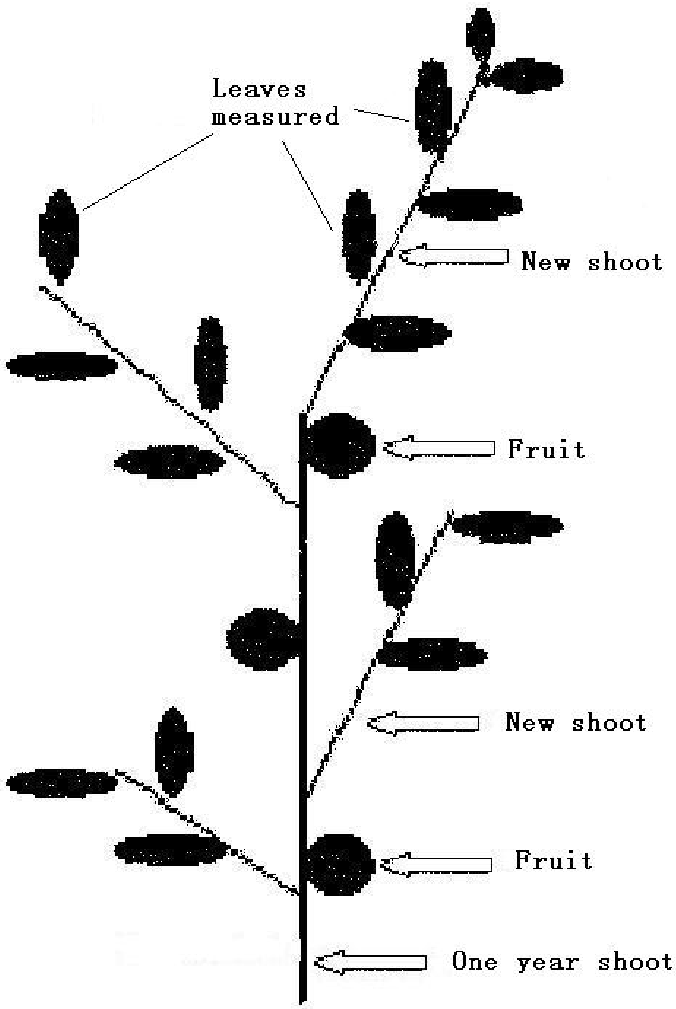

Figure 1. Leaves selected for measurement in this paper

grow continuously under low or high light condition, changes at biochemical, ultrastructural, anatomical or even morphological levels occur (Adamson et al., 1991). Plant adaptation to weak light is closely related to many internal and external factors. Plant light-saturated photosynthetic capacity, dark-adapted quantum efficiency of photosystem II and relative chlorophyll content are employed to characterize plant responses to different light conditions (Griffin et al., 2004). Plant shade tolerance is characterized by morphological and physiological traits that enhance the net rate of carbon capture in low light. For example, in shaded ginger plants (0 to 80% of full sunlight exposure), chloroplast size and leaf number decreased, while the leaf area, leaf thickness, the numbers of grana lamella, special grana lamella and starch grains increased (Zhang et al., 1999). The mesophyll thickness of poinsettia decreased significantly when shade increased from 30 to 92% (Galicia-Jimenez et al., 2001). Additionally, when plants grow under low light, the number of palisade cells, chlorophyll content, the ratio of chlorophyll a/b and the electron transfer rate declined. In cotton, low light radiation causes a significant decrease in both ribulose bisphosphate (RuBP) carboxylation efficiency and maximum regeneration rate (Yang et al., 2005). It was also reported that carbon allocation to roots is restricted under low light conditions (Paez et al., 2000). Griffin et al. (2004) suggested that photosynthesis rate, carbohydrate ability, chlorophyll content and the characteristics of chloroplast might be used as indices to assess the ability of plants under low PPFD.

Peach trees grow in greenhouses where solar radiation is weak because of shading film and overlapped canopies. In this study, we aimed to investigate the effects of low PPFD on leaf morphology, stoma density and chlorophyll content in leaf, leaf photosynthesis rate, and ribulose bisphosphate carboxylase (RuBPCase) activity in three different peach cultivars: *Prunus persica* L. Batsch ‘Qingfeng’ and Maixiang’, as well as *P. persica* var. nectarine ‘NJN76’, all of which are commonly planted in greenhouses.

MATERIALS AND METHODS

Plant materials and treatments

Three-year-old trees of *P. persica* L. Batsch ‘Qingfeng’, ‘Maixiang’ and *P. persica* var. nectarine ‘NJN76’ were used in the present investigation at Beijing University of Agricultural, Beijing, China. Peach seedlings each with ten leaves were transplanted into 30 × 40 cm clay pots containing 5.5 kg of fertile alluvial soil, one plant per pot. All pots were placed in a greenhouse (60 × 6 m). One year later, January 1, 2006, the following treatments were implemented: 1) non-shading, full sunlight exposure (CK), and 2) 80% of full sunlight exposure (T1). All peach trees were covered with the same double layer shading film from the top, so that the expected FFFD in T1 were maintained at canopies. LI-1400 data logger and quantum sensor Li-190SA were used to observe the PPFD for each treat-ment. Triple replications were arranged in randomized blocks and there were 10 potted trees for each of two different shading treatments. All the peach trees were irrigated with Murashige and Skoog (MS) solution. The fully expanded, upper canopy leaves were selected for anatomical study, photosynthetic study and other studies as indicated Figure 1 (Kong et al., 2007).

Net photosynthesis rate

Net photosynthesis rate (Pn) was measured one month after shading treatment started using a portable photosynthesis system (LI-6400, Li-Cor, Lincoln, NE, USA). It was measured at 400 ± 10 μmol mol^{-1} CO_2 concentrations in the inflowing air, ambient relative humidity 60 ± 5 % and leaf temperature of 25℃. Data were collected from 6:00 to 18:00 h. The leaves for net photosynthesis rate measurement were as shown in Figure 1.

Chlorophyll content

Six mature leaves as showed in Figure 1 were selected for chlorophyll content determination immediately after photosynthetic rate was measured; the leaves were sampled, homogenized with 15 ml of 95% ethanol and centrifuged at 3000 ×g for 5 min. The upper solution was measured with a UV-2001 spectrophotometer at 645 and 663 nm. Chlorophyll content was calculated as described by Arnon (1949).

Table 1. Changes in chlorophyll a (Chla), chlorophyll b (Chlb) contents [mg g^{-1}(FM)], stoma density (number mm^{-2}), stoma aperture (μm) and stoma conductance (μmol $m^{-2}s^{-1}$) in leaves of peach plants grown under non-shading, full sunlight exposure (CK) and 80% of full sunlight exposure (T1).

Cultivar	Treatment	Chl*b* (mg /g_{FM})	Chl*a* (mg/g_{FM})	Stoma density (/mm^2)	Stoma conductance (μmol/ m^2s^1)
Qingfeng	CK	0.20b	0.28a	324a	0.33a
	T1	0.23a	0.32a	298b	0.24b
Maixiang	CK	0.24b	0.31b	277a	0.35a
	T1	0.39a	0.42a	260b	0.27b
NJN76	CK	0.23b	0.30a	301a	0.33a
	T1	0.26a	0.36a	276b	0.24b

For each treatment, statistical differences among irradiance treatments were analyzed by LSD test. Values followed by different letters are significantly different ($p < 0.05$).

Stoma density and aperture

Mature leaves as defined in Figure 1 were selected for the present investigation of stoma density and aperture according to Olmez et al. (2006).

Leaf area and leaf mass per unit area

Leaf area was measured using CID CAF1-CI-203 leaf area instrument. For dry mass (DM) determination, samples were first kept at 110℃ for 15 min and then maintained at 80℃ until constant mass. Leaf mass per unit area (LMA) was calculated as leaf dry mass/leaf area.

Ultrastructure of chloroplast

For chloroplast ultrastructure investigation, the mature leaves were cut into small pieces (0.5 x 0.5 mm) and immediately fixed in 5% glutaraldehyde (in sodium-cacodylate buffer, pH 7.2) for 3 h as described by Pilarski (1993). The specimens were sectioned and stained with uranium acetate-lead citrate, observed and photographed under a JEM-100 CX transmission electron microscope.

Photosynthetic O_2 evolution rate

Photosynthetic O_2 evolution rate was measured with a Clark-type oxygen electrode (Hansatech, King's Lynn, UK) under white light with a saturating PPFD (800 µmol m^{-2} s^{-1}) as described by van Gorkom and Gast (1996).

ATPase and RuBPCase activities

The activities of Ca^{2+}-ATPase and Mg^{2+}-ATPase were analyzed according to Liu and Hao (1990) and Cai et al. (1980). Ribulose bisphosphate carboxylase (RuBPcase) activity and nicotinamide adenine dinucleotide phosphate hydrogen (NADPH) content were determined according to Khanna-Chopra (1982) and Ye and Zhao (1990), respectively.

Statistics

Results represented the average of independent experiments in three replicates. Data were analyzed using the statistical analysis systems (SAS). Each plant from an individual treatment was taken as a replicate. The means of each parameter were compared among treatments using a one way analysis of variance (ANOVA) in the General Linear Model Procedure of SPSS (version 12, SPSS, Chicago, IL, USA). Least significant differences (LSD) were considered between individual treatments when the F-test of the ANOVA was significant at $p < 0.05$.

RESULTS

Chlorophyll content

Peach leaf chlorophyll contents significantly increased under 80% PPFD when compared with their corresponding controls in the unshaded treatment (Table 1): leaf Chl*a* content of 'Maixiang' increased by 20.8%, 'Qingfeng' and 'NJN76' increased by 15.0 and 13.0% respectively. Nevertheless, whether shaded or not, leaf Chl*a* content of 'Maixing' was the highest among all the three cultivars. The variation pattern of Chl*b* was the same as Chl*a* under 80% PPFD among all cultivars.

Stoma

Stoma density in 'Maixiang' at 80% PPFD decreased moderately (277 to 260 number mm^{-2}) when compared with the decreases in 'Qingfeng' (from 324 to 250 number mm^{-2}) and 'NJN76' (301 to 243 number mm^{-2}). The response of stoma apertures and stoma conductance due to shade were similar to those in stoma density. Shading had less effect on 'Maixiang' stoma density, stoma aperture and stoma conductance than that of 'Qingfeng' and 'NJN76'.

Leaf morphological characteristics

Compared with the non-shade control, leaf areas and LMA values of all the three cultivars at 80% PPFD decreased with little significant difference (Table 2). Shading at 80% PPFD, decreased LMA values in 'Qingfeng' and 'NJN76' was more than that of 'Maixiang', 'Maixiang' still has the highest LMA values among all the

Table 2. Changes in leaf areas (cm^2), leaf mass per unit area (LMA) (mg cm^{-2}), upper epidemic thickness (UET) (µm), lower epidemic thickness (LET) (µm), palisade tissue thickness (PTT) (µm) and sponge tissue thickness (STT) (µm)] in leaves of peach plants grown under non-shading, full sunlight exposure (CK) and 80% of full sunlight exposure (T1).

Cultivar	Treatment	Leaf area (cm^2)	LMA (mg/cm^2)	UET (µm)	LET (µm)	PTT (µm)	STT (µm)
Qingfeng	CK	34	6.35	13.2	13.0	50.5	62.3
	T1	31.3 HS	4.3 HS	10.2 HS	10.3 S	55.5 HS	60.3 NS
Maixiang	CK	33.6	6.4	13.1	13.0	54.6	64.0
	T1	30.8 HS	5.2 HS	10.2HS	9.2 HS	57.6 NS	59.8 NS
NJN76	CK	34.4	6.5	14.3	12.7	55.4	66.9
	T1	29.7 HS	3.90 HS	10.8 HS	9.4 HS	59.8 NS	61.3 NS

For each treatment, statistical differences among treatments were analyzed by T test. Values followed by different letters indicated significance of $P \leq 0.01$ (HS), $P \leq 0.05$ (S) and P (NS), respectively.

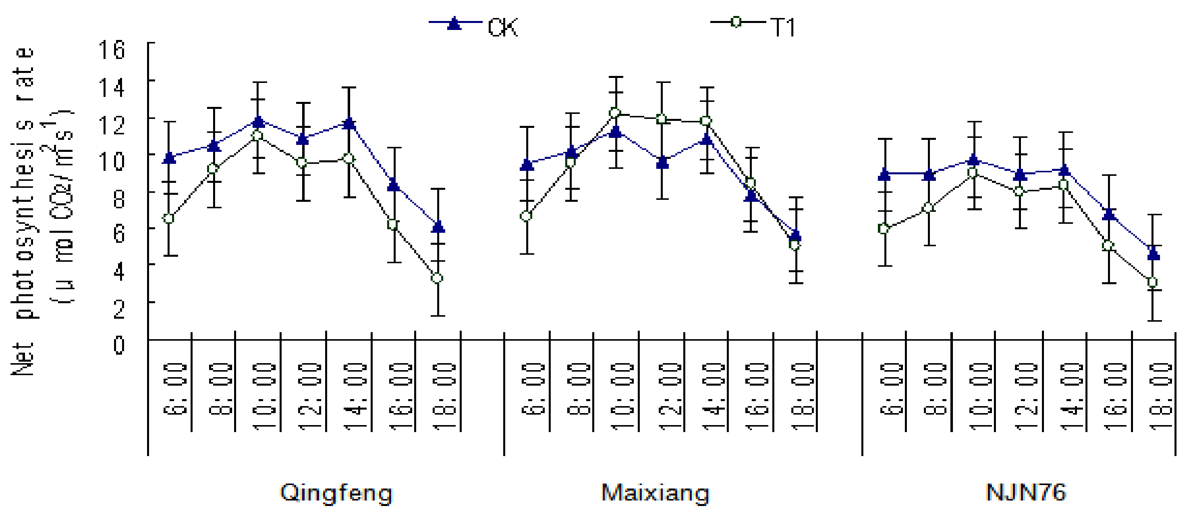

Figure 2. Effect of shading on net photosynthesis rates of three peach cultivars grown under greenhouse of non-shading, full sunlight exposure (CK, control, filled triangle) and 80% of full sunlight exposure (T1, open rhombus). The data represent the means ± SE of nine replicates.

cultivars. Thickness of leaf upper or lower epidermis also decreased slightly among all the three cultivars, no obvious difference was observed among them. At 80% PPFD, the thickness of palisade tissue increased, the thickness of sponge tissue reduced, but there was no significant difference among all the cultivars.

Net photosynthesis rate

It is interesting to note that although Pn of shade plants was lower than their corresponding control plants (Figure 2), at 80% PPFD, 'Maixiang' still exhibited a slightly higher photosynthesis rate between 10:00 and 14:00 than the other two cultivars, suggesting that 'Maixiang' was more tolerant to low PPFD.

RuBPcase activity

Leaf ribulose bisphosphate carboxylase (RuBPcase) activities of 'Maixiang' and 'Qingfeng' were higher than that of 'NJN76' when not shaded (Table 3); while under 80% PPFD, leaf RuBPcase activity in 'Maixiang', 'Qingfeng' and 'NJN76' all declined. However, the RuBPcase activity in 'Maixiang' was slightly higher than that of 'Qingfeng' and 'NJN76'.

Ca^{2+}-ATPase and Mg^{2+}-ATPase activity

Shade decreased the activities of Ca^{2+}-ATPase and Mg^{2+}-ATPase in the three cultivars (Table 3), whereas Ca^{2+}-ATPase activity of 'Maixiang' was still significantly higher than that of 'NJN76' and 'Qingfeng' at 80% PPFD. This suggest that 'Maixiang' was more suitable to low light conditions than both 'Qingfeng' and 'NJN76'.

NADPH content

The pattern of response in NADPH content among the

Table 3. Changes of ribulose bisphosphate carboxylase activities (RuBPcase) [$\mu molCO_2.min^{-1}g^{-1}_{FW}$], Ca^{2+}- and Mg^{2+} adenosinetriphosphatase activities (Ca^{2+}- and Mg^{2+}-ATPase) [$\mu mPi \cdot mg^{-1}_{chl}$], nicotinamide adenine dinucleotide phosphate contents (NADPH) [$nmol.mg^{-1}$] and photosynthetic O_2 evolution rates [$\mu mol.O_2g^{-1}_{FW}hr^{-1}$] in leaves of peach plants grown under non-shading, full sunlight exposure (CK) and 80% of full sunlight exposure (T1).

Cultivar	Treatment	RuBPcase activity ($\mu molCO_2.min^{-1}g^{-1}_{FW}$)	Ca^{2+}-ATPase activity ($\mu mPi \cdot mg^{-1}_{chl}$)	Mg^{2+}-ATPase activity ($\mu mPi \cdot mg^{-1}_{chl}$)	NADPH content ($nmol.mg^{-1}_{chl}$)	Photosynthetic O_2 evolution rate ($\mu mol.O_2g^{-1}_{FW}hr^{-1}$)
Qingfeng	CK	6.01a	756.3a	702.2a	5.08a	163.2±7.3
	T1	5.01b	665.7b	609.2b	4.18b	95.1±5.0
Maixiang	CK	6.00a	735.7a	678.9a	4.62a	138.0±7.1
	T1	5.34a	702.8b	643.7b	3.91b	129.0±4.3
NJN76	CK	5.47a	742.1a	693.3a	4.40a	91.8±6.1
	T1	4.12b	604.5b	501.8b	3.580b	74.1±6.8

For each treatment, statistical differences among treatments were analyzed by LSD test. Values followed by same letters in the same column are of not significantly different ($p < 0.05$).

cultivars was the same as that of Ca^{2+}-ATPase and Mg^{2+}-ATPase activity, suggested that 'Maixiang' was more adapted to lower light conditions (Table 3).

Photosynthetic O_2 evolution rate

Photosynthetic O_2 evolution rate of 'NJN76' was the lowest among the three cultivars under non-shade, followed by 'Maixiang' and 'Qingfeng' (Table 3). Eighty percent PPFD markedly decreased the photosynthetic O_2 evolution rates of the three cultivars, but 'Maixiang' still remained the highest photosynthetic O_2 evolution rate among all the three cultivars.

DISCUSSION

Low PPFD, photosynthesis rate and plant growth

In response to reduced PPFD, peach leaf area increased, shade-grown leaves were thinner, flatter and darker green than sun-grown ones (Nii and Kuroiwa, 1988). In the present study, we observed that the leaf areas of all cultivars decreased due to shading treatments, which contrasts with the findings of Nii and Kuroiwa (1988), who reported that the shade increased peach leaf area. Perhaps different treatments and different PPFD resulted in different conclusion. However, other workers have reported that at low PPFD, there is a characteristic increase in grana stacking, with no change in chlorophyll a/b ratio in ornamental aroids and increased chlorophyll content per unit leaf area and per dry weight (Zhang et al., 1999). But in the present investigation, we observed an increase in chlorophyll content as the intensity of shading increases. This is supported by the observations of Galicia et al. (2001) who found that chlorophyll content of poinsettia increa-ses steadily with shading. In this study, light affected peach leaf stoma aperture size and stoma conductance, and stoma density decreases with shading (Lenny et al., 2004).

The reduced chlorophyll content and stoma conductance contributed to the decreased photosynthesis rate at 80% PPFD. It is interesting to note that at 80% PPFD stoma density, conduc-tance and aperture size in 'Maixiang' declined less than that of 'Qingfeng' and 'NJN76', and the ability to maintain higher photosynthesis rate at 80% PPFD suggested that 'Maixiang' might be more tolerant to low light condition than the other two peach cultivars.

Low PPFD, ATPase and RuBPcase activity

Adenosine triphosphate (ATP) is an important cofactor of RuBPcase in isolated chloroplasts. ATPase activity and the extent of oligomerization of RuBPcase are closely linked. RuBPcase oligo-merization is highly specific for Mg^{2+}-ATP, and exhibits a response to ATP concentration, being inhibited by ADP (Liu et al., 2006). The concen-tration of Mg^{2+} in the chloroplast stroma is light-dependent and is of regulatory significance for other reactions of the Benson-Calvin cycle. Illumi-nation generates an increase in the concentration of stroma Mg^{2+} (Sumio et al., 2004) and the stromal ATP/ADP quotient (Sumio et al., 2004). In the present study, the RuBPcase activity was coupled with Ca^{2+}- and Mg^{2+}- ATPase activities. Shading at 80% PPFD led to a decrease in the activities of RuBPcase, Ca^{2+}- and Mg^{2+}- ATPase, but much less in 'Maixiang' than in the other two cultivars, suggesting again, that 'Maixiang' would be more suitable for indoor greenhouse conditions.

The activity of RuBPcase, carbohydrate rate and electron transport rate has previously been reported (Zhou et al., 2007). At low PPFD, the reduced photosynthetic O_2 evolution rate was probably due to the suppression of RuBPcase activity, leading to decreased carbon fixation. In the present investigation, though RuBPcase activity of all the three cultivars decreased due to shading treatment, RuBPcase activity in 'Maixiang' was still the highest among all the tested cultivars.

Low PPFD and NADPH

There was a strong correlation between PPFD, electron transport rate and NADP-MDH activation. Decreased $NADPH/NADP^+$ ratio has two main implications for carbon fixation. Firstly, the lack of reducing equivalents limits the ribulose bisphosphate (RuBP) regeneration. Secondly, the consumption of adenosine triphosphate (ATP) may be severely restricted, thus compensating for the decreased rate of ATP synthesis. As reported previously (Zhou et al., 2007), the decreased CO_2 assimilation rate in plants is associated with reduced RuBP concentration. The reason for the decreased RuBP concentration is straight forward: the reduced amount of NAPDH forms a bottleneck in the regeneration pathway and occurs with low light. In our study, we noticed that under low light, the NADPH contents in all the three peach declined. It was assumed that low light induced the decrease of electron transport rate in the plants, subsequently leading to the decreased synthesis of ATP and NADPH and further impairing RuBP regeneration capacity. Among the three cultivars tested, all the indices tested in 'Maixiang' decreased less than the other two cultivars, indicating that 'Maixiang' was more suitable for greenhouse conditions than the other two cultivars.

In summary, our present study strongly suggests that compared with 'Qingfeng' and 'NJN76', 'Maixiang' was more adaptive to lower light, with a slightly reduced Chl*a* content, stoma density, stoma aperture size, stoma conductance, LMA and chloroplast number, all contributed to the less decreased photosynthesis rate when shaded at 80% PPFD. Hence, 'Maixiang' is the best cultivar to be planted in greenhouse when the sunlight is low.

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