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Cyanide-resistant respiratory pathway is involved in the high-light systemic acquired acclimation of kidney bean (*Phaseolus vulgaris*)

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Abstract

After exposing one half of a low light-adapted kidney bean (*Phaseolus vulgaris*) leaf to high light, parameters of chlorophyll (Chl) *a* fluorescence, such as PSII operating efficiency, PSII maximum efficiency under light, and photochemical quenching, decreased in the opposite half of the same leaf, whereas the capacity of the cyanide-resistant respiratory pathway significantly increased. When one half of the low light–adapted leaf was exposed to low light, the opposite half pretreated with 1 mM salicylhydroxamic acid (SHAM, an inhibitor of the cyanide-resistant respiratory pathway) did not exhibit significant changes in the Chl fluorescence values compared with the without SHAM pretreatment. However, after exposing one half of the low light–adapted leaf to high light, the opposite half pretreated with 1 mM SHAM showed lower Chl fluorescence values than that without SHAM pretreatment. Our results indicate that partial exposure of the low light–adapted leaf to high light can impose a systemic stress on the PSII photochemistry. The enhanced capacity of the cyanide-resistant respiratory pathway may be involved in the maintenance of the photosynthetic performance in the leaf tissues experiencing high light–induced systemic stress.

Additional key words: bean leaf; chlorophyll fluorescence; salicylhydroxamic acid.

Introduction

In photosynthetic organs, light energy is transformed into reducing equivalents, which is used for CO_2 fixation or reductive biosynthetic reactions. However, under the condition of high light (HL) irradiation, the production of reducing equivalents generally exceeds that required by the plant and it causes over-reduction of PSII in the chloroplasts. Under such conditions, there is an increased risk that molecular oxygen is reduced to reactive oxygen species, which can cause oxidative stress to chloroplasts and other cellular components (Osmond 1981, Powles 1984, Maxwell *et al.* 1999).

Plants have evolved many mechanisms that allow acclimatory responses to HL stress. Previous studies have demonstrated that plants can dissipate the excessive reducing equivalents produced under HL by photorespiration, cyclic electron flow, and nonphotochemical quenching (NPQ) (Bauwe *et al.* 2010, de Bianchi *et al.* 2010, Gordon *et al.* 2013, Johnson 2011). In addition, a part of these excessive reducing equivalents can be imported into mitochondria *via* the malate/oxaloacetate shuttle and can be dissipated by the mitochondrial respiratory chain (Raghavendra and Padmasree 2003). The mitochondrial respiratory chain in higher plants involves two ubiquinol-oxidizing pathways. One is the cytochrome respiratory pathway that generates the proton-motive force used for ATP synthesis; another one is the cyanide-resistant respiratory pathway that channels the electrons directly from ubiquinone to O_2 and, thus, is uncoupled from ATP synthesis (Siedow and Umbach 2000, Foyer and Noctor 2002). The cyanide-resistant respiratory pathway (CRRP) is considered to dissipate the excessive reducing equivalents more efficiently than the cytochrome respiratory pathway, because the operation of the CRRP is not restricted by the proton gradient across the

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Abbreviations: CRRP – cyanide-resistant respiratory pathway; HL – high light; HL SAA – high-light systemic acquired acclimation; HS – HL+SHAM; LL – low light; LS – LL+SHAM; NPQ – nonphotochemical quenching; F_v'/F_m' – PSII maximum efficiency under light; POD – peroxidase; q_P – photochemical quenching; SHAM – salicylhydroxamic acid; V_{alt} – capacity of cyanide-resistant respiration; Φ_{PSII} – PSII operating efficiency.

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mitochondrial inner membrane and by the cellular ATP/ADP ratio (Yoshida *et al.* 2006, 2007).

In the natural environment, sometimes only a part of a leaf (or plant) can be subjected to HL due to the angle of the sun and shade from clouds or neighboring leaves (Gordon *et al.* 2013). It has been found that such conditions cause photo-oxidative stress not only in the tissues directly experiencing HL, but also in the tissues still under shade [*i.e.*, in parts of the leaf (or plant) that do not directly experience HL]. Moreover, acclimation of metabolism in the tissues that do not directly experience HL also occurs (Karpinski *et al.* 1999, Gordon *et al.* 2013). This phenomenon is termed "high-light systemic acquired acclimation" (HL SAA) (Karpinski *et al.* 1999, Gordon *et al.* 2013). Researches over the last decades revealed some important determinants involved in HL SAA, such as the induction of antioxidant defenses (Karpinski *et al.* 1999). However, whether the CRRP is involved in HL SAA stays still unknown.

In the present work, one half of the low light-adapted kidney bean (*Phaseolus vulgaris*) leaf was illuminated with HL to induce a systemic stress in the opposite half of the leaf that was still maintained under low light. Under such conditions, we investigated possible involvement of the CRRP in HL SAA.

Materials and methods

Plants and culture condition: Seeds of kidney bean (*Phaseolus vulgaris* L. Nongpu.12) were sterilized with 1% NaClO for 10 min and then washed with distilled water 5–6 times to remove the remaining NaClO. The seeds were germinated at 26°C on damp gauze. The germinated seeds were planted and grown in plastic pots containing loam soil:perlite [2:1 (v/v)] under 120 μmol(photon) m^{-2} s^{-1}, 14 h light/10 h dark cycles at 25°C. Two- to three-week-old-seedlings with fully expanded, primary leaves were used for experiments.

Treatments of bean leaves: At the end of a 14-h light period, the fully expanded, primary leaves were exposed to a low light (LL) intensity [40 μmol(photon) m^{-2} s^{-1}] for 2 h to adapt to the changes of conditions. Then one half of the LL-adapted leaf was infiltrated with 1 mM SHAM (diluted with water from a 0.4 M stock in ethanol) using a needleless syringe (Gilliland *et al.* 2003). After infiltration, the leaf was incubated for 2 h to inhibit the CRRP. As a control, the ethanol solution (< 1%, v/v) with the concentration equivalent to that in the 1 mM SHAM diluted from the stock was infiltrated alone into one half of the LL-adapted leaf under the same conditions (Fig. 1*A*). We excluded the possibility that SHAM could cross the midrib from the infiltrated half to the opposite half of the leaf. It was proved by the observation that infiltration of one half of the leaf with 1 mM SHAM did not affect the cyanide-resistant O_2 uptake in the other half of the same leaf (data not shown). After this treatment, the leaf with the petiole was cut and placed in a 1-mL tube with some water to prevent desiccation. Then, the leaf was inserted horizontally through a slit (as long as the long axis of the leaf) of a vertical cardboard frame, and the long axis of the leaf was fixed into the slit (Fig. 1*B*). This position enabled to maintain the infiltrated half of the detached leaf still under LL, while the other half was exposed to LL or high light (HL)[about 1,800 μmol(photon) m^{-2} s^{-1}] for 40 min (Fig. 1*A*) in a temperature-controlled water bath containing a water layer that enabled the air temperature to remain the same. The cardboard frame was sufficiently thick and slit was sufficiently narrow to avoid the direct effect of HL on the infiltrated half of the same leaf. After this treatment, the infiltrated half, which was still maintained under LL, was used for the measurements of respiration and Chl fluorescence.

As described in the Fig. 1*A*, when the right half of a LL-adapted leaf was exposed to LL or HL, the opposite left half, which was infiltrated with the solvent of 1mM SHAM and still maintained under LL, was called LL-leaf or HL-leaf, respectively. When the right half was exposed to low light or high light, the opposite left half, which was infiltrated with 1 mM SHAM and still maintained under low light, was called as the LS-leaf or HS-leaf, respectively.

Treatment	Conditions	
LL	Low light	40 μmol(photon) m^{-2} s^{-1}
HL	High light	1,800 μmol(photon) m^{-2} s^{-1}
LS	LL+SHAM	40 μmol(photon) m^{-2} s^{-1} 1 mM salicylhydroxamic acid
HS	HL+SHAM	1,800 μmol(photon) m^{-2} s^{-1} 1 mM salicylhydroxamic acid

Leaf respiration: The leaf tissue was cut into small pieces, suspended immediately in the assay buffer containing 20 mM HEPES and 0.2 mM $CaCl_2$ (pH 7.2), and incubated in the dark for 10 min to allow wound respiration to subside. The capacity of the CRRP of the leaves (V_{alt}) was measured by a Clark-type oxygen electrode (*SP-2 type, Institute of Plant Physiology & Ecology*, *Chinese Academy of Sciences*, China) at 25°C according to previous work (Feng *et al.* 2013). The residual respiration was measured in the assay buffer containing 5 mM SHAM plus 1 mM KCN (Bingham and Farrar 1989). V_{alt} was obtained and calculated as the difference between the leaf oxygen uptake in the presence of 1 mM KCN and the residual respiration and was expressed as [μmol(O_2) g^{-1}(FM) min^{-1}].

Chl fluorescence parameters were measured at room temperature (25°C) using a portable fluorometer (*PAM 2500*,

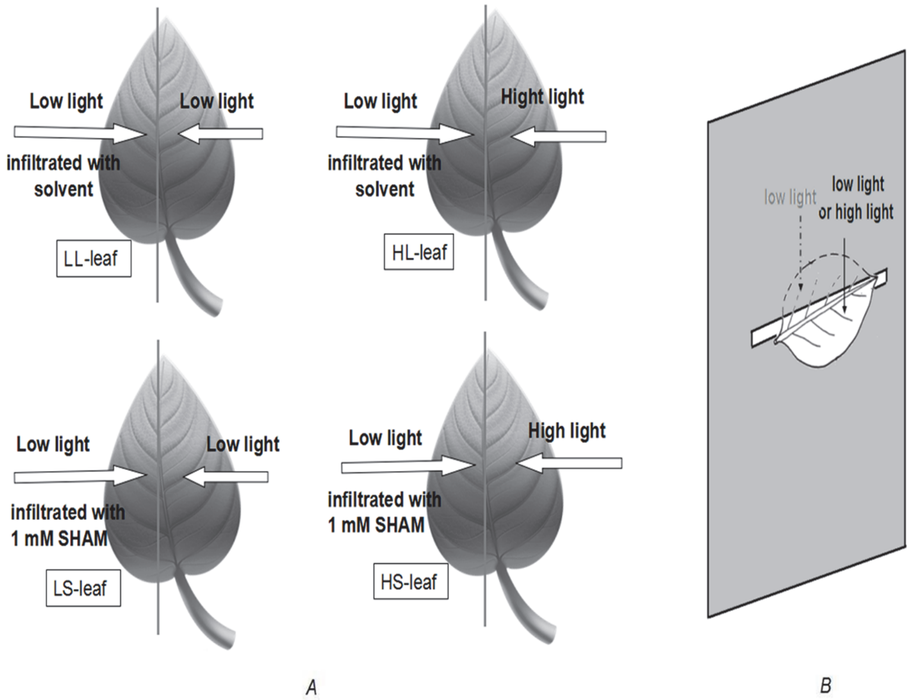

Fig. 1. *A*: Treatment of bean leaves. *B*: Detached leaf, inserted horizontally through a slit of a vertical cardboard frame and fixed into the slit. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

Walz, Germany). The fluorescence yield at steady-state photosynthesis at any given irradiance (F_s) was determined. After this, the light-adapted maximum fluorescence yield (F_m'), which is produced by a 0.5-s saturating flash, was measured. Minimal fluorescence of the light-adapted state (F_0') was then determined with a far-red pulse in absence of the actinic light. The PSII operating efficiency was defined as $\Phi_{PSII} = (F_m' - F_s)/F_m'$, the PSII maximum efficiency under light was defined as $F_v'/F_m' = (F_m' - F_0')/F_m'$, and photochemical quenching was defined as $q_P = (F_m' - F_s)/(F_m' - F_0')$ (Possell *et al.* 2010).

Peroxidase activity: The leaf tissue was ground in 100 mM sodium phosphate buffer at pH 7.0 in a ratio of 5 mL(buffer) g^{-1}(leaf fresh mass, FM). After centrifugation at 11,600 × *g* in a centrifuge (*LGR16-W*, *Beijing Medical Centrifuge Factory*, China), the supernatant was used immediately as a crude enzyme extract. Each reaction mixture (1 mL) consisted of 10 µL of the enzyme extract and 990 µL of guaiacol solution containing 0.25% guaiacol (v/v) in 10 mM sodium phosphate buffer and 0.125% H_2O_2 (v/v). Peroxidase (POD, EC 1.11.1.7) activity in the extracts was measured as an increase in absorbance at 470 nm (Cipollini 1998). For calculation of POD activities, the molar extinction coefficient of 26.6 mM^{-1} cm^{-1} was used, and the activity was expressed as [mM min^{-1} g^{-1}(FM)].

Statistical analysis: The results are expressed as means ± standard deviation (SD). The data were statistically evaluated with *t*-test methods. The difference was considered to be statistically significant when $P<0.05$.

Results

Effects of HL on PSII photochemistry: We compared the difference of the Chl fluorescence parameters between the LL-leaf and HL-leaf. The results showed that the values of Φ_{PSII}, F_v'/F_m', and q_P tended to decline more in the HL-leaf than in the LL-leaf. The values of Φ_{PSII} and F_v'/F_m' in the HL-leaf significantly decreased by 11.9% and 11.8%, respectively, compared with the LL-leaf (Figs. 2,3). The value of q_P in the HL-leaf was also lower (but not significantly) compared to that in the LL-leaf (Fig. 4).

Effects of HL on the capacity of CRRP: We showed that the V_{alt} in the HL-leaf significantly increased compared with the LL-leaf (Fig. 5). The V_{alt} was 1.7 fold higher in the HL-leaf relative to the LL-leaf. This observation indicated that HL induced a systemic increase in the capacity of the CRRP in the leaf tissues that were indirectly experiencing HL.

SHAM inhibition of CRRP in LL-leaf and HL-leaf: In order to further investigate whether the CRRP could be involved in the acclimatory responses of leaf to the HL-induced systemic stress, SHAM, a well-known inhibitor of the CRRP (Chivasa and Carr 1998, Bartoli *et al.* 2005, Yoshida *et al.* 2006) was used in the present work. We used the concentration of SHAM that was reported to be sufficiently low to avoid possible side effects of this inhibitor and with no direct effects on photosynthetic O_2 evolution and Chl fluorescence parameters (Amor *et al.*

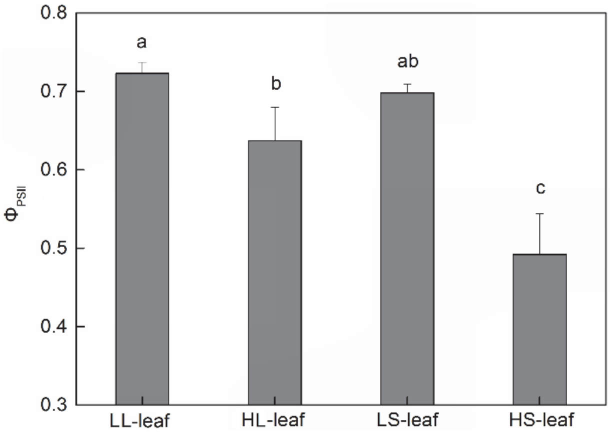

Fig. 2. The comparison of the PSII-operating efficiency (Φ_{PSII}) in the LL-leaf, HL-leaf, LS-leaf, and HS-leaf. Each value represents the mean ± SD (vertical bars) of four independent experiments. *Different letters* denote significant differences at $P<0.05$. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

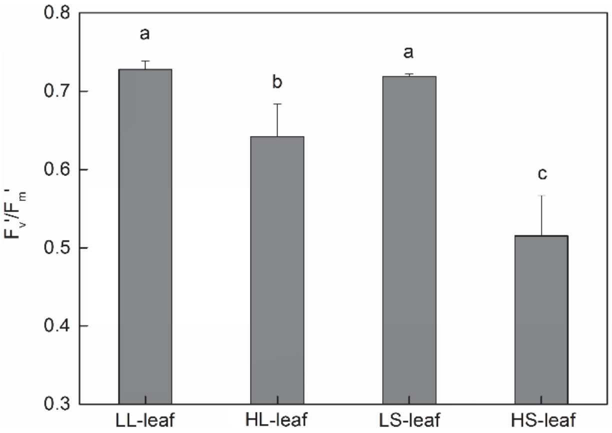

Fig. 3. The comparison of the PSII maximum efficiency under light (F_v'/F_m') in the LL-leaf, HL-leaf, LS-leaf, and HS-leaf. Each value represents the mean ± SD (vertical bars) of four independent experiments. *Different letters* denote significant differences at $P<0.05$. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

there were no significant differences in the values of Φ_{PSII}, 2000, Bartoli *et al*. 2005, Yoshida *et al*. 2006). Application of 1 mM SHAM inhibited the cyanide-resistant oxygen consumption of the LL-leaf and HL-leaf by 47.2% and 48.1%, respectively (Fig. 5).

Influence of SHAM on PSII photochemistry of LL-leaf and HL-leaf: Chl fluorescence parameters showed that

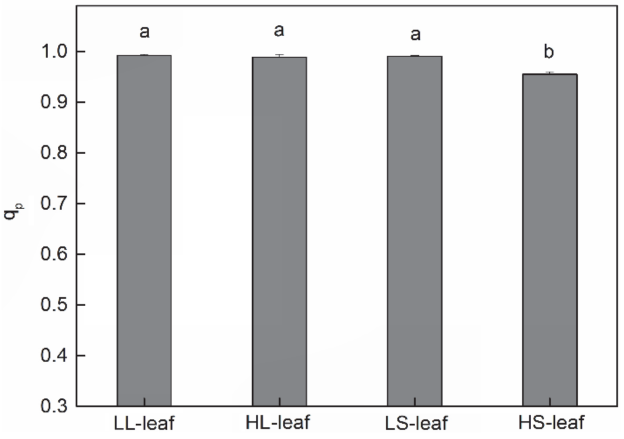

Fig. 4. The comparison of the photochemical quenching (q_P) in the LL-leaf, HL-leaf, LS-leaf, and HS-leaf. Each value represents the mean ± SD (vertical bars) of four independent experiments. *Different letters* denote significant differences at $P<0.05$. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

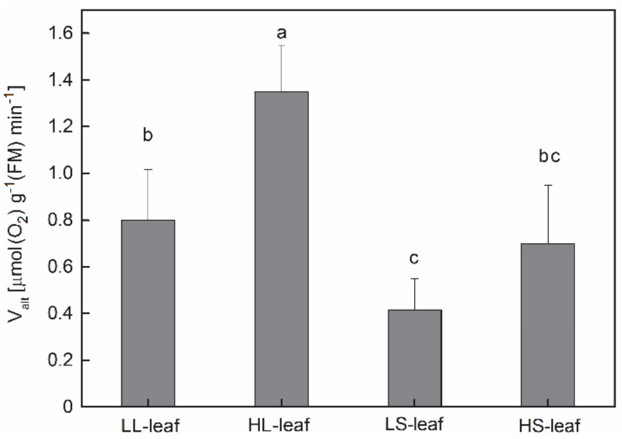

Fig. 5. The comparison of the capacity of the cyanide-resistant respiratory pathway (V_{alt}) in the LL-leaf, HL-leaf, LS-leaf, and HS-leaf. Each value represents the mean ± SD (vertical bars) of four independent experiments. *Different letters* denote significant differences at $P<0.05$. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

q_P, and F_v'/F_m' between the LL-leaf and LS-leaf (Figs. 2,3,4). However, the values of Φ_{PSII}, F_v'/F_m', and q_P in the HL-leaf significantly decreased by 22.8%, 19.8%, 3.4%, respectively, after the SHAM treatment. The values of Φ_{PSII}, F_v'/F_m', and q_P in the HS-leaf were also significantly lower than those in the LL-leaf (Figs. 2,3,4).

Discussion

Φ_{PSII} is an estimate of the proportion of photons used in photochemistry (Maxwell and Johnson 2000). F_v'/F_m' provides an estimation of the maximum quantum efficiency of PSII photochemistry in the illuminated leaf when Q_A is maximally oxidized and thus it can also be used to assess the contributions of nonphotochemical quenching (NPQ) to changes in the PSII-operating efficiency (Baker *et al*. 2007). A decrease in both $\Phi_{PSII,}$ and

F_v'/F_m' reflected that the ability of PSII to utilize light energy in photochemistry decreased. Thus, compared with the LL-leaf, the lower values of Φ_{PSII} and F_v'/F_m' in the HL-leaf (Figs. 2,3) indicated that partial exposure of the LL-adapted leaf to HL resulted in a systemic stress of PSII in the unexposed regions of the leaf.

The q_P can be used to estimate the proportion of oxidized PSII centres (Maxwell and Johnson 2000). Commonly, the proportion of oxidized PSII centres trends to decrease when PSII suffers from stress (Havaux *et al.* 1991, Lima *et al.* 2002). However, it did not seem to occur here, since q_P in the HL-leaf exhibited only a slight, but insignificant, decrease compared to that in the LL-leaf (Fig. 4).

Previous studies have shown that HL stress induces an increase in the capacity of the CRRP, in alternative oxidase protein (AOX, which catalyzes the cyanide-resistant respiratory pathway), and/or in AOX mRNA content. It was suggested that the CRRP can avoid over-reduction of PSII, and, thus, alleviate the HL-induced stress in the chloroplasts of the plant cells that are directly experiencing HL (Yoshida *et al.* 2006, 2007, Bartoli *et al.* 2005, Zhang *et al.* 2010). Our results showed that HL could induce a systemic increase in the capacity of the CRRP in leaf tissues that were indirectly experiencing HL (Fig. 6). It is possible that when a partial region of a leaf is exposed to HL, some specific components could be produced and imported into the adjacent tissues to stimulate the capacity of the CRRP. Further study is required to investigate the mechanism for such a systemic increase in the CRRP capacity under HL.

Although there were no significant differences in the values of Φ_{PSII}, q_P, and F_v'/F_m' between the LL-leaf and LS-leaf, the values of the Chl fluorescence parameters in the HS-leaf were significantly lower than those in the HL-leaf (Figs. 2,3,4). Although SHAM has been reported to inhibit the activity of POD at higher concentration (20 mM), the effect of SHAM at low concentration (2 mM) was minimal (Amor *et al.* 2000). We also found that 1 mM SHAM had no significant effects on the activity of POD either in the LL-leaf or HL-leaf (Fig. 6). Some studies reported that the AOX inhibitors, such as *n*-propyl gallate, would also inhibit the activity of the plastid terminal oxidase (PTOX) of the chloroplast (Cournac *et al.* 2002). However, many researches have revealed that SHAM has no significant influence on O_2 evolution rates and Chl fluorescence parameters of intact chloroplasts (Bartoli *et al.* 2005, Yoshida *et al.* 2006), suggesting that SHAM does not directly affect the enzyme activities of chloroplasts. In addition, the activity of PTOX in the light is very low and most electrons from plastoquinol are diverted to PSI, rather than to PTOX (Ort and Baker 2002, Kuntz 2004, Yoshida *et al.* 2006). Thus, we suggest that the significant decrease in Φ_{PSII}, F_v'/F_m', and q_P in the HS-leaf was mainly attributed to the inhibition of cyanide-resistant respiration. Although the decrease in the Chl fluorescence parameters in the HS-leaf seemed to be moderate, it should be noted that 1 mM SHAM inhibited cyanide-resistant oxygen consumption of the HL-leaf only by 48.1% (Fig. 5). It is expected that a higher or complete inhibition of the cyanide-resistant respiration in the HS-leaf would cause a more dramatic decrease in the Chl fluorescence parameters. We assume that when HL induces a systemic stress in PSII, the increased capacity of CRRP could be utilized to alleviate the systemic stress and prevent the over-reduction of PSII in the leaf tissues, which are indirectly experiencing HL.

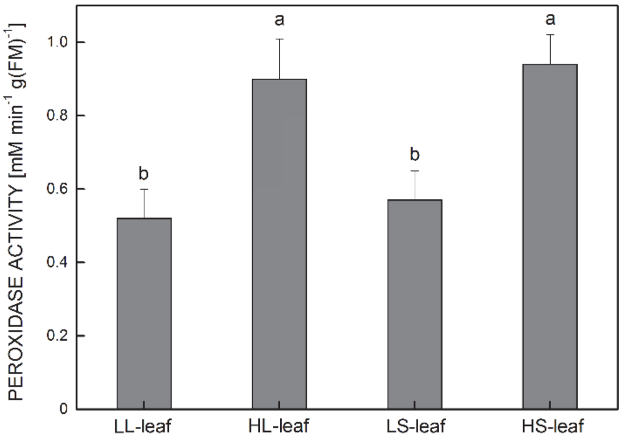

Fig. 6. The comparison of the activity of peroxidase in the LL-leaf, HL-leaf, LS-leaf, and HS-leaf. Each value represents the mean ± SD (vertical bars) of four independent experiments. *Different letters* denote significant differences at $P<0.05$. LL – low light; HL – high light; LS – low light +SHAM; HS – high light +SHAM.

Because the electrons flowing through the cytochrome respiratory pathway can be redirected to the CRRP by addition of cyanide (Vanlerberghe and McIntosh, 1992), the measured values of V_{alt} (in the presence of KCN) and the reduced V_{alt} after SHAM treatment do not necessarily represent the actual level or changes in activity of the CRRP (Florez-Sarasa *et al.* 2011). Interestingly, Florez-Sarasa *et al.* (2011) found that under HL stress [800 μmol(photon) m^{-2} s^{-1} for 8 h], the photosynthetic electron transport rate and q_p in wild-type and *AOX1a* antisense *Arabidopsis* lines were lower than those in an *AOX1a* overexpressing line. However, the *AOX1a* overexpressing line only showed the higher capacity of the CRRP than that in the wild-type and *AOX1a* antisense lines, while the activity of the CRRP (measured by oxygen isotope fractionation) was similar in all three lines (Florez-Sarasa *et al.* 2011). Therefore, an increase in the capacity of the CRRP seems to be important for the maintenance of the photosynthetic performance under HL stress. Nevertheless, oxygen isotope fractionation technique could help elucidate the role of the CRRP more precisely.

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