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ORIGINAL ARTICLE

The decline in photosynthetic rate upon transfer from high to low light is linked to the slow kinetics of chloroplast ATP synthase in *Bletilla striata*

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Abstract
Upon a sudden transition from high to low light, the rate of CO_2 assimilation (A_N) in some plants first decreases to a low level before gradually becoming stable. However, the underlying mechanisms remain controversial. The activity of chloroplast ATP synthase (g_H^+) is usually depressed under high light when compared with low light. Therefore, we hypothesize that upon a sudden transfer from high to low light, the relatively low g_H^+ restricts ATP synthesis and thus causes a reduction in A_N. To test this hypothesis, we measured gas exchange, chlorophyll fluorescence, P700 redox state, and electrochromic shift signals in *Bletilla striata* (Orchidaceae). After the transition from saturating to lower irradiance, A_N and ETRII decreased first to a low level and then gradually increased to a stable value. Within the first seconds after transfer from high to low light, g_H^+ was maintained at low levels. During further exposure to low light, g_H^+ gradually increased to a stable value. Interestingly, a tight positive relationship was found between g_H^+ and ETRII. These results suggested that upon a sudden transition from high to low light, A_N was restricted by g_H^+ at the step of ATP synthesis. Taken together, we propose that the decline in A_N upon sudden transfer from high to low light is linked to the slow kinetics of chloroplast ATP synthase.

Keywords CO_2 assimilation · Chloroplast ATP synthase · Electron transport · Fluctuating light · ATP synthesis · Photosynthetic reduction

Introduction

Under natural field conditions, plants are challenged by frequent fluctuations of light levels (Yamori 2016). Upon a sudden transition from high to low light, the net rate of CO_2 assimilation (A_N) in some species, e.g., *Glycine max* (soybean) and *Arabidopsis thaliana*, first declined and then slowly increased to a stable value (Chen and Xu 2006; Armbruster et al. 2014; Sakowska et al. 2018). This photosynthetic reduction significantly affect plant productivity (Zhu et al. 2004; Sakowska et al. 2018). Currently, two schemes are used to explain this transient decrease in A_N: (1) the slow downregulation of thermal energy dissipation decreases electron flow through photosystem II (PSII) (Zhu et al. 2004; Armbruster et al. 2014, 2016) and (2) the slow re-association of the light-harvesting complex of PSII (LHCII) to PSII complexes (Chen and Xu 2006; Betterle et al. 2009; Xu et al. 2015). As we know, the slow downregulation of thermal energy dissipation and re-association of LHCIIs to PSII complexes are common phenomena in higher plants. However, in some plants such as wheat and pumpkin, A_N dropped immediately to a stable value after a sudden transfer from high to low light (Chen and Xu 2006). Therefore, the mechanisms underlying the sudden decrease in A_N remain controversial.

Under high light, a high proton gradient (ΔpH) across the thylakoid membranes activates energy-dependent quenching (qE) to harmlessly dissipate absorbed light energy in the PSII antenna as heat (Müller et al. 2001; Munekage et al. 2002). Thus, qE can decrease the energy transfer to PSII by

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up to 75% under high light (Demmig-Adams et al. 2012). Upon the transition from high to low light, qE is downregulated. However, this downregulation needs several minutes (Zaks et al. 2012), leading to the scheme that photosynthesis upon transfer from high to low light is limited by the slow relaxation of non-photochemical quenching (Zhu et al. 2004; Armbruster et al. 2014). In the model plant *A. thaliana*, K^+ efflux antiporter 3 (KEA3) allows proton efflux from the thylakoid lumen to stroma, accelerating the downregulation of NPQ after the transition from high to low light, increasing linear electron flow (LEF) and A_N (Armbruster et al. 2014, 2016; Höhner et al. 2019). Furthermore, owing to the lack of protein PsbS, A_N significantly increased in the first 40 s after the transition from high to low light, as shown in the *psbs* mutant when compared with the wild type (Armbruster et al. 2014). Interestingly, although overexpression of KEA3 largely accelerates the downregulation of NPQ, it has little effect on the photosynthetic rate during the transition from high to low light (Armbruster et al. 2014). Therefore, the sudden decrease in photosynthesis cannot be wholly explained by the slow downregulation of qE. Because proton motive force (*pmf*) plays a key role in regulation of linear electron flow at the Cyt b_6/f complex (Suorsa et al. 2016; Armbruster et al. 2017; Yang et al. 2019), the immediate reduction in A_N after that transition may be due to the regulatory effect of *pmf* on LEF. However, little is known about the change in *pmf* after transition from high to low light.

During further exposure to low light, the gradually increase in A_N was accompanied with the increase in LEF (Armbruster et al. 2014), indicating that A_N is determined by LEF. In LEF, electrons derived from water splitting in PSII are transported to $NADP^+$ via plastoquinone (PQ), the cytochrome b_6/f (Cyt b_6/f) complex, plastocyanin, and PSI. This electron transport is coupled to proton translocation and generates a *pmf* that drives ATP synthesis via chloroplast ATP synthase (Kramer et al. 2003, 2004). As a result, LEF produces ATP and NADPH for the CO_2 assimilation. However, if ATP were to be consumed at a greater rate than NADPH, LEF would rapidly become limiting by the lack of $NADP^+$, decreasing rates of ATP regeneration and photosynthesis (Walker et al. 2014). Therefore, we speculate that the photosynthetic reduction upon a sudden transfer from high to low light may be caused by the imbalance between ATP production and consumption.

After a sudden transition from high to low light, the whole leaf ATP level first decreased and then gradually increased in Spinach (Stitt et al. 1989). In chloroplast, *pmf* drives the phosphorylation of ADP to ATP in chloroplast CF_0CF_1-ATP synthase (Sacksteder et al. 2000; Hahn et al. 2018). The conductivity of the chloroplast ATP synthase to protons (g_H^+) is modulated to regulate *pmf* and ΔpH under changing environments (Kanazawa and Kramer 2002; Kohzuma et al. 2009; Zhang et al. 2009; Takagi et al. 2017; Huang et al. 2017). Recent studies indicated that g_H^+ decreases under high light when compared with under low light (Takagi et al. 2017; Huang et al. 2018c). After transfer from high to low light, g_H^+ gradually increased to a stable value, which needed approximately 2 min (Huang et al. 2018a). Therefore, upon a sudden transition from high to low light the relatively low g_H^+ theoretically restricts ATP synthesis, making ATP to be consumed at a greater rate than NADPH. As a result, A_N will rapidly become limiting by the lack of ATP. Thus, we hypothesize that the transient decrease in A_N after transition from high to low light may be linked to the low value of g_H^+.

Here, we focused on the mechanisms underlying the transient decrease in A_N after transition from high to low light. Our aims were to (1) examine the change in *pmf* during this transition and (2) test the hypothesis that the transient decrease in A_N is linked to g_H^+. To address these questions, we examined gas exchange, PSI and PSII parameters, and the electrochromic shift signals after transition from high to low light in *Bletilla striata*.

Materials and methods

Plant materials and growth conditions

In our preliminary experiment, we observed that *Bletilla striata* (Orchidaceae) showed a transient decrease in A_N after transition from high to low light. As a result, in this study, we used 2 years old plants of *B. striata* for experiments. Plants were grown in a greenhouse with high relative air humidity (60–70%) and 40% of full sunlight. Growth light condition was controlled by using non-woven shade net. During growth periods, the maximum light intensity at noon was approximately 800 µmol photons m^{-2} s^{-1}. These plants were not subjected to water or nutrition stresses. Intact mature leaves were used for the photosynthetic measurements.

Gas exchange measurements

The data for net CO_2 assimilation rate (A_N) and stomatal conductance (g_s) were measured using Li-6400XT (Li-Cor Biosciences, Lincoln, NE, USA) and a 2-cm^2 measuring head (6400-40 Leaf Chamber Fluorometer; Li-Cor Biosciences). Measurements were made in a greenhouse where the relative air humidity and air temperature were approximately 60% and 25 °C, respectively. The atmospheric CO_2 concentration was controlled at 400 µmol mol^{-1}. When leaves displayed steady-state high levels of photosynthesis and g_s after light adaptation at 1000 µmol photons m^{-2} s^{-1} for 20 min, light response curves were measured, with photosynthetic parameters being evaluated at 3-min intervals at PPFDs of 1000, 800, 600, 400, 200, 100, and 50 µmol photons m^{-2} s^{-1}. Photosynthetic performance during the transition from high

to low light was examined by first illuminating leaves at 923 µmol photons m^{-2} s^{-1} for 20 min. Afterward, the actinic light was decreased to 132 µmol photons m^{-2} s^{-1}. Those two light intensities, e.g., 923 and 132 µmol photons m^{-2} s^{-1}, were set according to the actinic light in the Dual PAM-100 (Heinz Walz, Effeltrich, Germany).

Chlorophyll fluorescence and P700 measurements

PSI and PSII parameters were recorded simultaneously at 25 °C using the Dual PAM-100 (Heinz Walz, Effeltrich, Germany). The light response curves were generated by first illuminating the leaves at 923 µmol photons m^{-2} s^{-1} for 20 min to obtain steady-state conditions. Afterward, the light-adapted photosynthetic parameters were recorded after exposure for 3 min to light intensities of 923, 611, 421, 272, 132, and 59 µmol photons m^{-2} s^{-1}. The PSI and PSII parameters during the transition from saturating to limiting light were investigated by illuminating dark-adapted leaves at 923 µmol photons m^{-2} s^{-1} for 20 min and then exposing them to 132 µmol photons m^{-2} s^{-1} for 6 min.

PSII parameters were calculated as follows (Baker 2008): $Y(II) = (F_m' - F_s)/F_m'$ (Genty et al. 1989), and $NPQ = (F_m - F_m')/F_m'$. F_m and F_m' represent the maximum fluorescence after dark and light adaptation, respectively. F_s is the light-adapted steady-state fluorescence. F_m was determined after dark adaptation for at least 30 min. Y(II) was defined as the effective quantum yield of PSII, while NPQ indicated the non-photochemical quenching in PSII. Photosynthetic electron flow through PSII was calculated as $ETR\,II = PPFD \times 0.5 \times 0.84 \times Y(II)$.

The PSI photosynthetic parameters were measured as described by Schreiber and Klughammer (2008). The quantum yield of PSI photochemistry was calculated as $Y(I) = (P_m' - P)/P_m$; the quantum yield of PSI non-photochemical energy dissipation due to the donor-side limitation, $Y(ND) = P/P_m$; and the quantum yield of PSI non-photochemical energy dissipation due to the acceptor-side limitation, $Y(NA) = (P_m - P_m')/P_m$. Photosynthetic electron flow through PSI was calculated as $ETRI = PPFD \times 0.5 \times 0.84 \times Y(I)$.

Electrochromic shift (ECS) analysis

The ECS signal was monitored as the change in absorbance at 515 nm, using a Dual PAM-100 equipped with a P515-analysis module (Klughammer et al. 2013; Wang et al. 2015; Takagi et al. 2017). Steady-state ECS signals at different actinic light (AL) intensities (132 and 923 µmol photons m^{-2} s^{-1}) were obtained after illumination for 20 min at each light level. Changes in the ECS signal during the transition from high to low light were examined by illuminating the leaves at 923 µmol photons m^{-2} s^{-1} for 20 min before adjusting the light intensity to 132 µmol photons m^{-2} s^{-1}. The ECS signal during illumination was obtained by switching off the actinic light for 1 s (Wang et al. 2015; Huang et al. 2018b). We analyzed ECS dark interval relaxation kinetics ($DIRK_{ECS}$) as described by Kramer group (Sacksteder et al. 2001; Cruz et al. 2005). The difference in total *pmf* between light and dark, ECS_t, was estimated from the total amplitude of the rapid decay of the ECS signal during the dark pulse. The slow relaxation of the ECS signal was measured to calculate ΔpH and ΔΨ. The value of g_H^+ was estimated as the inverse of the time constant of the first-order ECS relaxation (Sacksteder and Kramer 2000; Cruz et al. 2005).

Statistical analysis

The results were displayed as mean values of five independent experiments. *T*-test was used at the $\alpha = 0.05$ significance level to determine whether those results were significantly different between treatments.

Results

Light intensity dependence of PSI and PSII parameters

The light response changes in PSI and PSII parameters were first analyzed (Fig. 1). As expected, Y(I) and Y(II) decreased with an increase in light intensity (Fig. 1a, b). While Y(NA) was higher than Y(ND) at intensities below 200 µmol photons m^{-2} s^{-1}, above that light level, Y(NA) decreased and Y(ND) increased (Fig. 1a). As the illumination became more intense, NPQ was markedly increased and was saturated at approximately 600 µmol photons m^{-2} s^{-1} (Fig. 1b). The high levels of Y(ND) and NPQ under high light indicated the ΔpH-dependent energy dissipation and photosynthetic control at the Cyt b_6/f complex. While ETRII was saturated at 272 µmol photons m^{-2} s^{-1}, ETRI was saturated at 421 µmol photons m^{-2} s^{-1} (Fig. 1c). The large difference between ETRI and ETRII under high light suggested that activation of cyclic electron flow. It should be noted that these photosynthetic electron transport rates were calculated as $ETRI\ (or\ ETRII) = PPFD \times 0.5 \times 0.84 \times Y(I)\ (or\ Y(II))$, where 0.5 is the fraction of absorbed light reaching PSI or PSII (dI or dII). Based on this equation, ETRII was higher than ETRI when illuminated at low light. Actually, ETRI should be equal to or higher than ETRII at low light. As a result, the value of dI was higher than dII for leaves of *B. striata*.

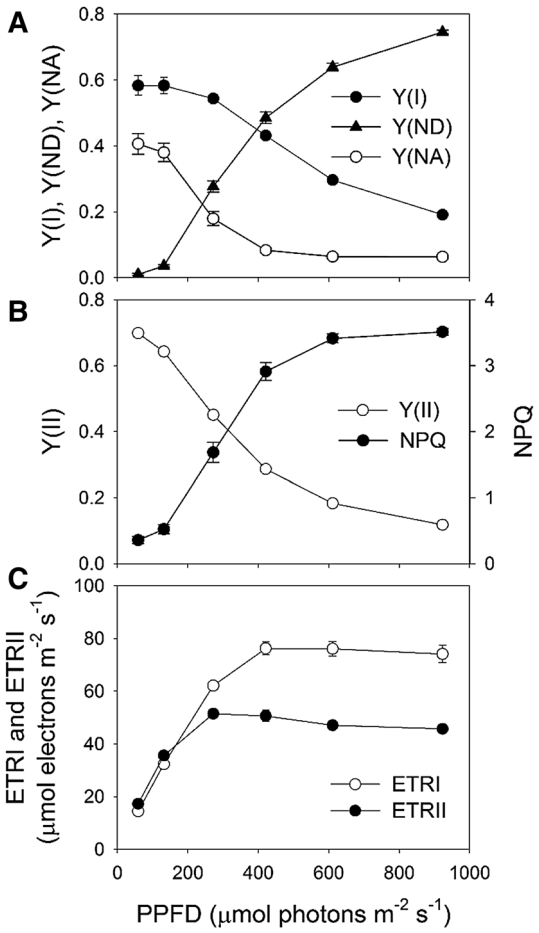

Fig. 1 Light intensity dependence of PSI and PSII parameters. Y(I), quantum yield of PSI photochemistry; Y(ND), quantum yield of PSI non-photochemical energy dissipation due to the donor-side limitation; Y(NA), quantum yield of PSI non-photochemical energy due to the acceptor-side limitation; Y(II), quantum yield of PSII photochemistry; NPQ, non-photochemical quenching in PSII; ETRI, electron transport rate through PSI; and ETRII, electron transport rate through PSII. Values are means ± SE ($n = 4$)

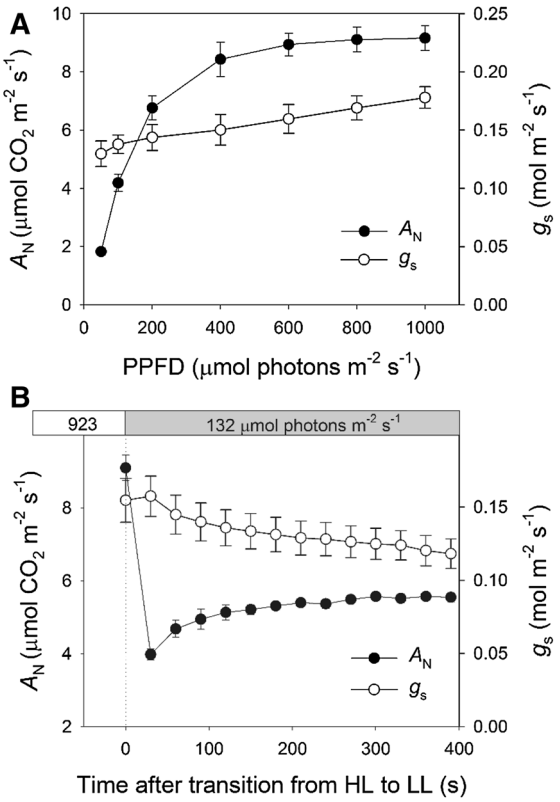

Fig. 2 **a** Light intensity dependence of net CO_2 assimilation rate (A_n) and stomatal conductance (g_s), and **b** changes in A_n and g_s after transition from 923 to 132 μmol photons m^{-2} s^{-1}. Values are means ± SE ($n = 4$)

The rate of CO_2 assimilation upon transfer from high to low light

The net rate of CO_2 assimilation (A_N) was saturated at approximately 400 μmol photons m^{-2} s^{-1} (Fig. 2a). The maximum value of A_N at 1000 μmol photons m^{-2} s^{-1} was 9.2 μmol CO_2 m^{-2} s^{-1} (Fig. 2a). In the light response curve, stomatal conductance gradually increased with light intensity (Fig. 2a). After a sudden transition from 923 to 132 μmol photons m^{-2} s^{-1}, A_N rapidly decreased within 30 s, from 9.1 to 4.0 μmol CO_2 m^{-2} s^{-1} (Fig. 2b). During further exposure to the low light, A_N gradually increased to a stable value being 5.5 μmol CO_2 m^{-2} s^{-1} (Fig. 2b). The sudden decrease and subsequent increase in A_N were not caused by the change in g_s because the lowest A_N was accompanied by a high g_s (Fig. 2b). This photosynthetic performance during the transition from high to low light is similar to that reported from *A. thaliana* and soybean (Chen and Xu 2006; Armbruster et al. 2014).

PSI and PSII parameters during the transition from high to low light

We also investigated PSI and PSII parameters when plants transferred from saturating light (923 μmol photons m^{-2} s^{-1}) to low light (132 μmol photons m^{-2} s^{-1}). Interestingly, after a sudden transition, ETRI rapidly decreased to a stable level in 80 s (Fig. 3a). Concomitantly, ETRII first decreased to a low level in 20 s and then gradually increased to a stable value in 5 min (Fig. 3a), which was consistent with the performance of A_N. During this transition from saturating to limiting light, Y(ND) rapidly decreased to a low level within the first 40 s, where it was then maintained (Fig. 3b). Because the value of Y(ND) is largely controlled by ΔpH, this result indicated that the strong lumen acidification under high light was quickly relaxed after transition to low light. Concomitantly, the relaxation of NPQ was lower than Y(ND) (Fig. 3b), suggesting a slow reversibility of qE during that transition.

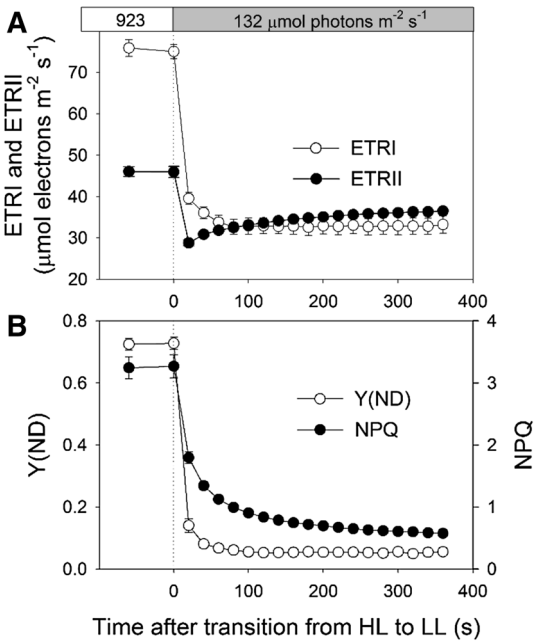

Fig. 3 Changes in ETRI, ETRII, Y(ND), and NPQ after transition from 923 to 132 µmol photons m^{-2} s^{-1}. Values are means ± SE (n = 4)

Proton motive force and g_H^+ during the transition from high to low light

To further examine whether the sudden decrease in A_N is caused by over-acidification of the thylakoid lumen, we first monitored the steady-state ECS signals at 923 and 132 µmol photons m^{-2} s^{-1}. Values for total *pmf*, ΔpH, and ΔΨ across the thylakoid membranes were significantly higher at 923 µmol photons m^{-2} s^{-1} (Fig. 4a). Furthermore, the portion of electric component ΔΨ/*pmf* increased at low light. These results suggested the stronger lumen acidification under high light. Concomitantly, g_H^+ was significantly lower at 923 µmol photons m^{-2} s^{-1} (Fig. 4a), indicating that proton conductivity of the thylakoid membranes was lower under high light. After transition from 923 to132 µmol photons m^{-2} s^{-1}, the *pmf* rapidly decreased to a low level where it was maintained over time (Fig. 4b). By comparison, g_H^+ was maintained at low levels within the first seconds and gradually increased to a stable level (Fig. 4b). We also calculated the change in proton influx (v_H^+) after transition from high to low light, and found that v_H^+ gradually increased and reached the maximum value at approximately 140 s (Fig. 4c). Furthermore, we found that, after this transition from high to low light, a tight positive linear relationship was found between g_H^+ and ETRII (Fig. 5). These results suggested that within the first seconds after transition from high to low light, the decreases in A_N and ETRII were caused by the low value of g_H^+.

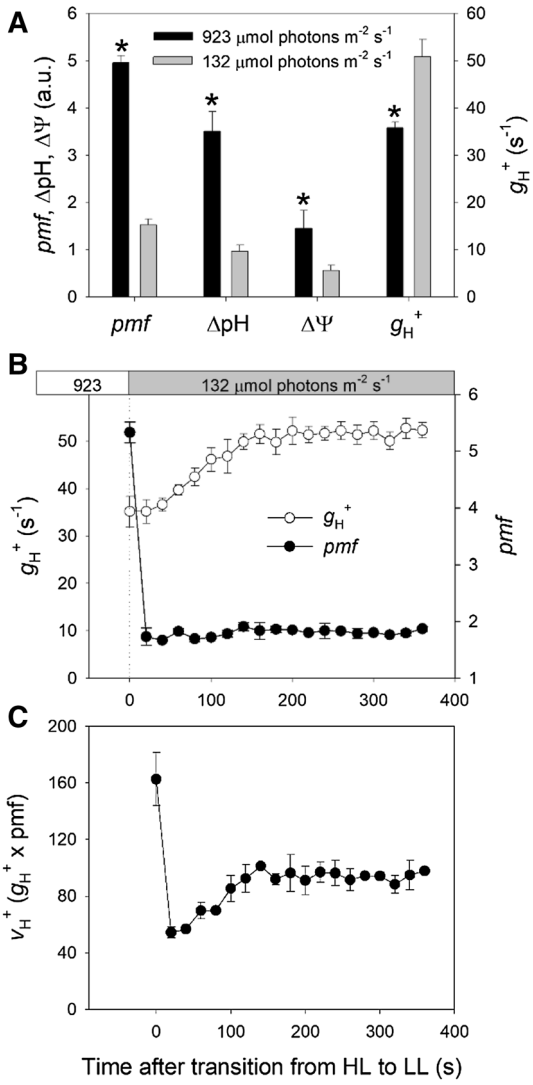

Fig. 4 **a** Steady-state values of proton motive force (*pmf*), proton gradient (ΔpH), membrane potential (ΔΨ), and proton conductivity (g_H^+) across the thylakoid membranes at 923 and 132 µmol photons m^{-2} s^{-1}. **b** Changes in *pmf* and g_H^+ after transition from 923 to 132 µmol photons m^{-2} s^{-1}. **c** Change in proton influx (v_H^+) (multiplying g_H^+ by *pmf*) after transition from 923 to 132 µmol photons m^{-2} s^{-1}. Values are means ± SE ($n = 4$). Asterisks indicate significant differences in results between different light levels

Discussion

In this study, we observed a transient decrease in A_N in *Bletilla striata* upon a sudden transition from high to low light (Fig. 2b). This phenomenon is called photosynthetic reduction at low light, resembling the phenotypes recorded from *Arabidopsis* and soybean (Chen and Xu 2006; Armbruster et al. 2014; Sakowska et al. 2018), although the underlying mechanisms have not yet been clarified. Some researchers have assumed that this sharp decrease in A_N is caused by the slow reversibility of ΔpH-dependent energy

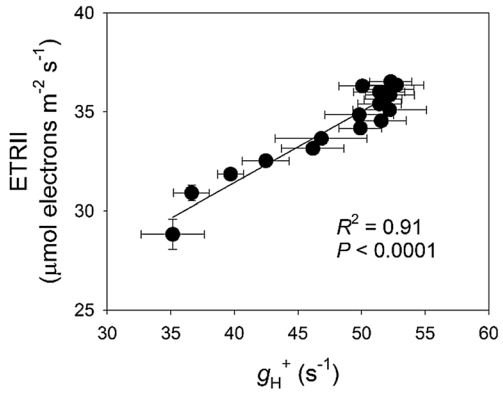

Fig. 5 Change in ETRII as a function of g_H^+ after transition from 923 to 132 μmol photons m^{-2} s^{-1}. Values are means ± SE (n = 4). All data were used from Figs. 3a and 4b

dissipation (Zhu et al. 2004; Armbruster et al. 2014, 2016). In addition, it is possible that this photosynthetic reduction may be linked to dissociation/re-association of some LHCIIs from/to PSII (Chen and Xu 2006). Although the slow reversibility of NPQ and re-association of LHCIIs to PSII are common phenomena in higher plants, A_N dropped immediately to a stable value in some plants such as cotton, maize, and pumpkin (Chen and Xu 2006). Therefore, these two previous schemes cannot wholly explain the sudden photosynthetic reduction upon transfer from high to low light.

In this article, we found that the sudden decrease in A_N was accompanied with the a low level of g_H^+, suggesting that the transient inactivation of chloroplast ATP synthase restricted A_N at the step of ATP synthesis. During further exposure to low light, the activity of chloroplast ATP synthase gradually increased to a stable value, increasing the rate of ATP synthesis (Fig. 4b). Meanwhile, A_N and ETRII gradually increased synchronously (Figs. 2b and 3a). Moreover, a tight linear positive relationship was found between g_H^+ and ETRII after transition from high to low light (Fig. 5). These results suggest that the decline in A_N upon transfer from high to low light is linked to the slow kinetics of chloroplast ATP synthase.

Under high light, ΔpH controls the oxidation of PQH_2 at the Cyt b_6/f complex, which limits electron flow from PSII to PSI, thus contributing to the oxidation of P700 (Munekage et al. 2002, 2004; Suorsa et al. 2012, 2016; Tikkanen and Aro 2014). As a result, the high levels of Y(ND) under high light are mainly caused by the enhancement of ΔpH across the thylakoid membranes (Yamamoto et al. 2016; Shikanai and Yamamoto 2017; Takagi et al. 2017; Huang et al. 2018d, 2019a). At low light, the reduced levels of ΔpH facilitate electron flow from PSII to PSI via the Cyt b_6/f complex, leading to smaller values for Y(ND) (Takagi et al. 2017; Huang et al. 2019b). We found that, after a sudden shift from high to low light, *pmf* rapidly decreased to a much lower level within the first 20 s and then remained stable over time (Fig. 4b). Meanwhile, Y(ND) largely decreased during the first 20 s (Fig. 3b), suggesting the rapid relaxation of ΔpH after that sudden transition. Under such conditions, the electron flow from PSII to $NADP^+$ would not have been limited by the oxidation of PQH_2 at the Cyt b_6/f complex. Consequently, the declines in A_N and ETRII during the transition from high to low light were independent of *pmf* and ΔpH.

Within the first seconds after transition from high to low light, the transient decrease in A_N was accompanied with reduced ETRII (Figs. 2b and 3a). During further exposure to low light, A_N and ETRII synchronously increased. These results suggested that the change in A_N after transition from high to low light was largely dependent on the performance of LEF. As we know, the depression of LEF can be caused by three aspects: (1) photoinhibition of PSI and PSII (Sejima et al. 2014; Brestic et al. 2015, 2016; Zivcak et al. 2015; Huang et al. 2018e); (2) over-acidification of thylakoid lumen (Livingston et al. 2010; Rott et al. 2011; Huang et al. 2018d); and (3) the lack of $NADP^+$ (Hald et al. 2008; Takagi et al. 2017). PSI and PSII are tolerant to short-term high light treatment in light-demanding plants (Barth et al. 2001; Yamori et al. 2016). As we know, NPQ is composed of energy-dependent quenching (qE), state transition quenching (qT), and photoinhibition quenching (qI). After transition from high to low light for 6 min, ETRII fully recovered to the maximum level. Therefore, after short-term adaptation at high light, the effect of photoinhibition on LEF could be eliminated. Furthermore, the *pmf* and ΔpH were rapidly relaxed within the first 20 s after transition from high to low light, preventing over-acidification of thylakoid lumen (Figs. 3b and 4b). Therefore, the sudden decrease in LEF was mainly caused by the lack of $NADP^+$.

Previous studies reported that g_H^+ was decreased by Pi deficiency in chloroplasts (Takizawa et al. 2008; Carstensen et al. 2018), indicating that chloroplast ATP synthase can be significantly modulated by the availability of ADP and Pi. In addition to Pi, thioredoxins and NADPH-dependent thioredoxin reductase (NTRC) plays an important role in redox regulation of the chloroplast ATP synthase specifically at low light (Naranjo et al. 2016; Carrillo et al. 2016). After transition from high to low light, the NADPH content rapidly decreased and NTRC gradually activated chloroplast ATP synthesis. In this article, we document that within the first seconds after transition from saturating to low light, g_H^+ is maintained at a low level (Fig. 4b), reducing the rate of ATP synthesis. Consistently, whole leaf ATP level rapidly decreased upon a sudden transition from high to low light (Stitt et al. 1989). As a result, at this moment, the ATP/NADPH production ratio is lower than the optimal ratio required by the primary metabolism. Consequently, the Calvin–Benson cycle is limited by the lack of ATP. Owing to the decreased rate of ATP production, ATP is consumed

at a greater rate than NADPH, and LEF is rapidly becoming limited by the lack of $NADP^+$. Consistently, ETRII is downregulated within the first seconds after transition from saturating to low light (Fig. 3a). This depression of LEF further decreases rates of proton translocation and ATP regeneration, leading to the restriction of A_N. Therefore, the sudden decrease in A_N upon transfer from high to low light is ultimately caused by the slow kinetics of g_H^+. During further exposure to low light, g_H^+ gradually increases (Fig. 4b), enhancing the rate of ATP synthesis and thus increasing the ATP/NADPH production ratio. Consequently, the availability of $NADP^+$ increases, facilitating the operation of LEF (Fig. 3a).

Conclusion

Photosynthetic performance under fluctuating light levels plays an important role in plant growth (Sakowska et al. 2018). After transfer from high to low light, the sudden decrease in A_N was observed in many studies (Zhu et al. 2004; Chen and Xu 2006; Armbruster et al. 2014). However, the underlying mechanisms have not yet been clarified. In this article, we found that the change in A_N after transfer from high to low light was positively correlated with the change in g_H^+. Under high light, g_H^+ significantly decreased due to Pi deficiency. Upon a sudden transition from high to low light, the low value of g_H^+ limited the rate of ATP synthesis, making A_N to be limited by the lack of ATP. Under such condition, LEF was rapidly limited by the lack of $NADP^+$. This depression of LEF further decreased the rate of ATP regeneration, reducing the light use efficiency. Taken together, we propose that the photosynthetic reduction upon transfer from high to low light is linked to the slow kinetics of g_H^+.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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