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BRIEF COMMUNICATION

Photoprotective roles of ascorbate and PSII cyclic electron flow in the response of the seagrass *Zostera marina* to oxygen-evolving complex photoinactivation

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Abstract

The oxygen-evolving complex (OEC) of *Zostera marina* is prone to deactivation under visible light, which results in a formation of the long-lived radical P_{680}^+. The mechanism to prevent damage caused by P_{680}^+ remains unclear. In this study, following light exposure, the upregulation in ascorbate (AsA) content and the presence of PSII cyclic electron flow (PSII-CEF) provide evidence that AsA and PSII-CEF donate electrons to PSII. Furthermore, a factorial design experiment with different combinations of inhibition of AsA and PSII-CEF demonstrates that both inhibition treatments lead to decreases in maximal photochemical yield of PSII, increases in relative variable fluorescence at the K-step, as well as the net loss of PSII reaction center proteins and further degradation of OEC peripheral proteins. These results suggest that AsA and PSII-CEF play photoprotective roles by providing electrons to efficiently prevent damage to PSII from the highly oxidizing radical P_{680}^+ in *Z. marina*.

Keywords: alternative electron donor; ascorbate; P_{680}^+; PSII cyclic electron flow; *Zostera marina*.

Seagrass, a unique taxon of marine plants, provides the foundation for highly productive marine ecosystems and habitats for various animal assemblages (Olsen *et al.* 2016). In the temperate northern hemisphere, *Zostera marina* is the dominant seagrass species; it evolved from a freshwater-living ancestor and returned into fully submerged marine conditions after migrating to a terrestrial environment, arguably the most dramatic habitat transition achieved by the flowering plants (Wissler *et al.* 2011). During its complex evolution, genes associated with stomata have been lost (Olsen *et al.* 2016); correspondingly, *Z. marina* chloroplasts are located in the epidermis of its leaves, ensuring sufficient transport or diffusion of inorganic carbon (Beer *et al.* 2014). However, this location of chloroplasts also ensures *Z. marina* chloroplasts receive maximum light exposure and the species is thus prone to photodamage (Beer *et al.* 2014). Additionally, ultraviolet, blue, and red/far-red light receptors are absent in *Z. marina* (Olsen *et al.* 2016). The loss of photoreceptors can weaken photoprotection and signaling functions, including insufficient anthocyanin shielding against high-energy wavelength damage (Li *et al.* 2013, Jiang *et al.* 2016).

Highlights

- Ascorbate (AsA) and PSII cyclic electron flow (PSII-CEF) donate electrons to PSII
- AsA and PSII-CEF efficiently prevent PSII reaction center damage from P_{680}^+
- AsA and PSII-CEF prevent PSII reaction center from disassembly

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Abbreviations: AsA – ascorbate; CEF – cyclic electron flow; DCPIP – dichlorophenol-indophenol; DMBQ – 2,5-dimethyl-p-benzoquinone; F_v/F_m – maximal photochemical yield of PSII; GLDH – l-galactono-1,4-lactone dehydrogenase; MR_{820nm} – 820-nm modulated reflection; OEC – oxygen-evolving complex; PSII-CEF – photosystem II cyclic electron flow; RbcL – Rubisco large subunit; RC – reaction center; $V_{re\text{-}red}$ – initial rate of P_{700}^+ re-reduction; W_K – PSII electron donation capacity.

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The lack of photoprotection by nonphotosynthetic epidermal cells and sunscreen compounds in *Z. marina*, in contrast to land plants, makes its chloroplasts more likely to confront high-energy wavelengths of light. Under these conditions, the oxygen-evolving complex (OEC), with absorption peaks ranging between UV and blue-green light wavelengths, is more vulnerable. Partial photoinactivation of OEC has been observed in our previous studies, as evidenced by both the increase in the relative variable fluorescence at the K-step (W_K) and the downregulation of OEC genes and proteins under light exposure (Yang *et al.* 2017, Tan *et al.* 2020a, Zhao *et al.* 2021a,b). Because water splitting releases electrons into the photosynthetic electron transport chain, continuous photoinactivation of OEC inevitably leads to insufficiency of electrons, interrupting the synthesis of ATP and NADPH. In addition, when the OEC electron donation rate is lower than the rate of electron withdrawal by the primary electron donor P_{680}, water-splitting dysfunction also leads to the formation of radical P_{680}^+, which can cause damage to the PSII reaction center (RC) components (Tyystjärvi 2008).

Our recent studies showed that limited electron resources are recycled through chloroplast NADPH dehydrogenase-like complex-dependent photosystem I cyclic electron flow (PSI-CEF), rather than being consumed through chlororespiration under light exposure, enabling chloroplasts to cope with the insufficiency of electrons (Tan *et al.* 2020a,b). Activated PSI-CEF contributes to the generation of ΔpH and ATP, thus maintaining a high ATP/NADPH ratio, which facilitates carbon assimilation. However, the mechanism that prevents damage caused by long-lived P_{680}^+ following OEC photoinactivation remains unclear.

When the OEC is impaired, either by heat stress or by UV-B exposure, ascorbate (AsA) is oxidized at the PSII donor side and plays a photoprotective role (Mano *et al.* 2004, Tóth *et al.* 2009, 2011). Considering that active OEC donates electrons with a half-time of about 0.1 to 1 ms whereas for AsA it is 20 ms (Tóth *et al.* 2009), it is unclear whether AsA can effectively prevent oxidative damage by P_{680}^+. As another electron transport event through P_{680}^+, PSII cyclic electron flow (PSII-CEF) is typically enhanced to consume excess energy when strong light and other factors, such as nitrogen limitation, lead to the over-reduction of the PSII acceptor side (Wagner *et al.* 2016). PSII-CEF also plays a vital role in drought-tolerant species *via* proton gradient formation without consumption of the limited water supply (Ananyev *et al.* 2017). Cytochrome b_{559}, a key PSII-CEF component, can provide electrons to PSII under PSII donor side impairment (Barber and De Las Rivas 1993, Magnuson *et al.* 1999, Shinopoulos and Brudvig 2012). Based on the assumption that both AsA and PSII-CEF can donate electrons to P_{680} in *Z. marina*, we investigated the responses of AsA and PSII-CEF following OEC photoinactivation and verified its photoprotective roles in preventing the damage to PSII caused by long-lived P_{680}^+ at both the spectral and protein levels.

Sample preparation: Healthy *Zostera marina* samples were collected from subtidal seagrass beds at a depth of 3 m near Rongcheng (37°16'N, 122°41'E), Shandong province, China. Samples were precultured at 15°C for 3 d in an aquarium. A 10/14-h light/dark photoperiod with a minimum saturation light intensity of 100 μmol(photon) m^{-2} s^{-1} was adopted. For the experimental treatment, each plant was 'standardized' to maintain a similar leaf morphology for all shoots. To ensure the consistency of sample ages, leaves were harvested from 2 cm above the sheath for experimental measurement.

Experimental design: Before experimental treatment, precultured *Z. marina* plants were dark-adapted overnight. Then, the leaves were exposed to a light intensity of 300 μmol(photon) m^{-2} s^{-1}, approximating the maximum midday light intensity at the collection site.

PSII-CEF was inhibited or enhanced *via* incubation with 2,5-dimethyl-p-benzoquinone (DMBQ; *TCI*, Tokyo, Japan) at a concentration of 125 or 62 μM, respectively (Ananyev *et al.* 2016, 2017). AsA synthesis was inhibited by incubation with 50 μM rotenone (*Sigma-Aldrich*, St. Louis, MO, USA) (Millar *et al.* 2003, Garmier *et al.* 2008), as shown in Fig. 1S (*supplement*). Although the chloroplast NADPH dehydrogenase-like complex was also sensitive to rotenone (Garmier *et al.* 2008), no significant effect of 50 μM rotenone on *Z. marina* PSI-CEF was observed as indicated by the initial rate of P_{700}^+ re-reduction ($V_{re\text{-}red}$; Fig. 2S, *supplement*). To test the roles of AsA and PSII-CEF, four different combinations of AsA and PSII-CEF inhibitions were conducted: Light, Light + Rotenone, Light + DMBQ, and Light + Rotenone + DMBQ. These four treatments formed the base of a factorial experimental design. Before exposure, *Z. marina* leaves saturated with filtered seawater or with the seawater solution containing inhibitors were incubated in the dark for 10 min at 15°C. Moreover, leaves treated with 125 μM DMBQ or 50 μM rotenone under darkness for 190 min showed no significant changes in the maximal photochemical yield of PSII (F_v/F_m; Fig. 3S, *supplement*), indicating there were no significant side effects of 50 μM rotenone and 125 μM DMBQ on *Z. marina*. A stock solution of 10 mM DMBQ and 25 mM rotenone was prepared with dimethyl sulfoxide at a concentration that had no significant effect on *Z. marina* as indicated by F_v/F_m (Fig. 4S, *supplement*).

Absorption measurement: AsA contents in chloroplasts were monitored by using a vitamin C assay kit (*Nanjing Jiancheng Bioengineering Institute*, Nanjing, China). Intact chloroplasts were isolated using a plant leaf crude chloroplast isolation kit (*GMS16004.1*, *GENMED*, Boston, USA, Shanghai branch – www.sh-genmed.com). The 0.5-g leaf tissue samples were ground in the lysis buffer included within the kit. Cell debris and leaf tissue were removed by filtration and the suspension was centrifuged at 200 × *g* for 5 min. After centrifugation of the supernatant at 1,000 × *g* for 10 min, the chloroplast precipitate was resuspended in the storage solution included in the kit. All of the above procedures were performed at 4°C. Chloroplast intactness was assessed by light microscopy (Walker *et al.* 1987), in which intact chloroplasts exhibited a bright halo and were highly refractive, whereas broken chloroplasts exhibited

a dull halo, were nonrefractive, and had a much darker interior. Three microscopic sights were observed and the intactness obtained by counting was approximately 85%.

Chlorophyll (Chl) *a* fluorescence measurement: The *M-PEA-2* instrument (*Hansatech*, Hercules, UK) was employed to simultaneously detect the kinetics of OJIP and MR_{820nm} and thus to determine the photochemical activity and dissect events in the electron transport chain (Strasser *et al.* 2010, Gururani *et al.* 2015). The standardization of OJIP was calculated as $V_t = (F_t - F_0)/(F_m - F_0)$. Changes in OJIP fluorescence rise kinetics were determined by calculating the difference value in variable fluorescence curves as $\Delta V_t = \Delta[(F_t - F_0)/(F_m - F_0)]$. The maximal photochemical yield of PSII and the PSII electron donation capacity were calculated as $F_v/F_m = (F_m - F_0)/F_m$ and $W_K = (F_K - F_0)/(F_J - F_0)$, respectively (Strasser 1997, Brestic *et al*. 2012). MR_{820nm} was assessed by observations of saturating red light eliciting a fast oxidation phase with the following reduction phase. To determine the dark reduction of P_{700}^+, the reflection at 820 nm was recorded following 100 s of illumination with far-red light (Zhang *et al.* 2011). The initial rate of P_{700}^+ dark reduction, $V_{re\text{-}red}$, was calculated to quantify PSI-CEF activity.

Western blotting: Western blotting was used to quantify the OEC extrinsic proteins PsbO, PsbP, and PsbQ as well as the terminal enzyme l-galactono-1,4-lactone dehydrogenase (GLDH) of AsA biosynthesis and the PSII RC proteins D1 and CP43. GLDH, which is located in mitochondria, was detected by using the whole leaf protein isolated as previously described (Jorrin-Novo 2014). The OEC extrinsic proteins located in photosynthetic membranes were detected by using intact chloroplasts obtained by the crude isolation kit. To determine the consistency of the loaded sample quantity, the contents of proteins and Chl were monitored (Porra *et al.* 1989). Corresponding antibodies (*Agrisera*, Vännäs, Sweden) were used to perform western blot analyses (Fristedt *et al.* 2009). Rubisco large subunit (RbcL) was employed as a control for equal loading. The immunoreactive bands visualized by a *Gel Doc XR+* system (*Bio-Rad*, CA, USA) were quantified using *Image Lab* software.

Statistical analysis: The statistical software *SPSS 22.0* (*IBM Corp*., Armonk, NY, USA) was used to perform statistical analyses. Each parameter was examined by analysis of variance (*ANOVA*).

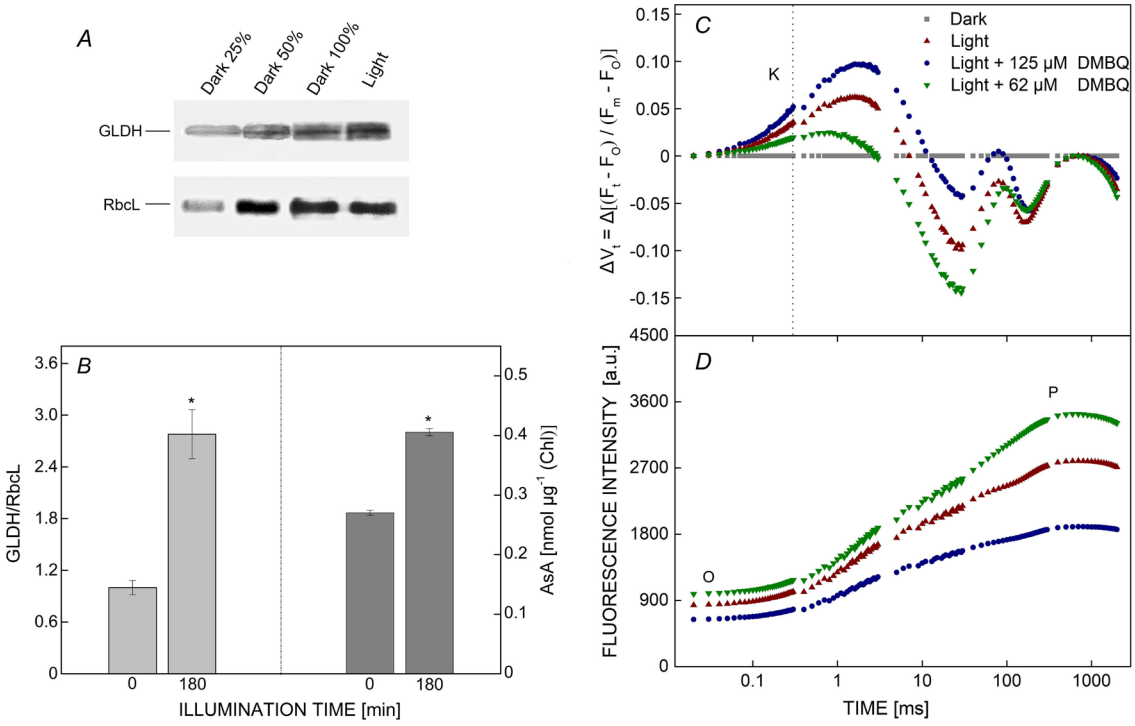

Fig. 1. Ascorbate (AsA) and PSII cyclic electron flow response to light exposure. (*A*) The changes in protein expression levels of l-galactono-1,4-lactone dehydrogenase (GLDH) during light exposure. To estimate the respective signal, a dilution series (0 min dark; 5, 10, and 20 µg of protein corresponding to 25, 50, and 100% of dark sample) of the *Zostera marina* proteins was applied on lanes 1–3. (*B*) Variations in GLDH contents determined by densitometric analysis and chloroplast AsA contents in response to light exposure. The significantly different value from 0 min (*Tukey*'s test, $P<0.05$) is marked with an asterisk (*). Data are expressed as mean ± SD ($n = 3$). Changes in chlorophyll *a* fluorescence kinetics as summarized by ΔV_t (*C*) and OJIP curves (*D*) in response to light exposure and different concentrations of DMBQ. The signals are plotted on a logarithmic time scale. Each curve represents the average of three replicates.

GLDH, the terminal enzyme in the major Smirnoff–Wheeler pathway for AsA biosynthesis, together with the AsA content in the chloroplasts were significantly upregulated after light exposure (Fig. 1*A*,*B*), providing a clue to AsA being an alternative electron donor. Additionally, analysis of the K-step in ΔV_t curves and F_P in OJIP curves showed that 125 μM DMBQ binding at the plastoquinone site, which uncouples PSII-CEF, induced a higher oxidation state of the PSII donor side and a lower PSII photochemical activity whereas 62 μM DMBQ binding at the Q_B site, which enhances PSII-CEF, induced the contrary change (Fig. 1*C*,*D*). These results suggest that PSII-CEF does exist and can provide electrons to PSII.

Generally, PSII-CEF is quantified by detecting the extent of the deficit in O_2 evolution (Lavaud 2007). However, the photoinactivation of OEC and the possible existence of another electron donation pathway in *Z. marina* would also lead to a decrease in O_2 evolution, making the change in O_2 evolution unable to fully reflect the activity of PSII-CEF. Moreover, owing to the lack of genetic tools in *Z. marina*, the physiological roles of AsA and PSII-CEF could not be examined by the gene knockout experiment. Thus, a factorial design experiment with different combinations of DMBQ and rotenone, specific inhibitors of PSII-CEF and AsA, respectively, was conducted to test the roles of AsA and PSII-CEF in safeguarding PSII function. Inhibition of AsA synthesis and uncoupling of PSII-CEF led to decreases in PSII electron donation capacity and PSII activity, as indicated by an increase in relative variable fluorescence at the K-step (W_K) and a decline in the maximal photochemical yield of PSII (F_v/F_m), respectively (Fig. 2*A*,*B*). Compared to W_K and F_v/F_m values, the order of activities were: Light > Light + Rotenone > Light + DMBQ > Light + Rotenone + DMBQ. With the continuous inactivation of OEC under light exposure (Tan *et al.* 2020b), the decreases became more obvious during late illumination (Fig. 2*A*,*B*). These results suggest that AsA and PSII-CEF function as alternative electron donors in PSII, supporting electron transport activity. Furthermore, western blot analyses showed no significant changes in D1 and CP43 protein levels after light exposure, and their degradation was detected after the suppression of electron donation (Fig. 2*C*), indicating that AsA and PSII-CEF efficiently prevent damage to PSII RC caused by P_{680}^+. The suppression of AsA and PSII-CEF also led to further impairment of OEC, as characterized by the distinct degradation of PsbO and PsbP proteins (Fig. 2*D*). The PSII RC disassembly

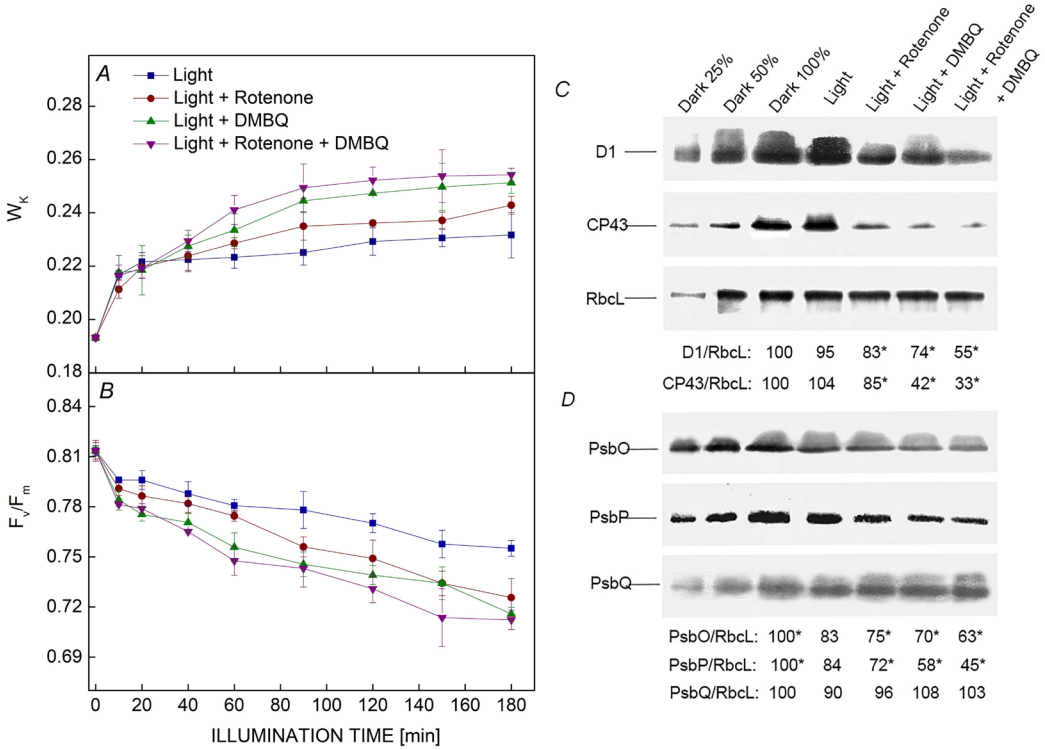

Fig. 2. Photoprotection of ascorbate and PSII cyclic electron flow response to light exposure. Time course of the changes in the relative variable fluorescence at the K-step (W_K) (*A*) and maximal photochemical yield of the PSII (F_v/F_m) (*B*) in response to different inhibitors. The significant effects of 50 μM rotenone and 125 μM DMBQ on F_v/F_m and W_K during HL exposure were examined with repeated measures *ANOVA* (all *P* values<0.05). The changes in PSII RC proteins D1, CP43 (*C*) and OEC peripheral proteins PsbO, PsbP, PsbQ (*D*) after 3 h of treatment. To estimate the respective signal, a dilution series (0 min dark; 2.5, 5, and 10 μg of chlorophyll corresponding to 25, 50, and 100% of dark sample) of the *Zostera marina* chloroplast proteins was applied on lanes 1–3. Values were % of dark 100% and normalized to RbcL amount. The significantly different value from light treatment (*Tukey*'s test, *P*<0.05) is marked with an asterisk (*). Data are expressed as mean ± SD (*n* = 3).

indicated by the parallel loss of PSII RC proteins and OEC peripheral proteins suggests that AsA and PSII-CEF protect PSII from severe photodamage.

In the case of electron insufficiency caused by OEC photoinactivation, reactive oxygen species (ROS) are unlikely to be formed. AsA, which can both eliminate ROS and donate electrons to PSII, may only play a role in supplying electrons in *Z. marina*. This view is also supported by our previous study, which showed that there was no significant change in antioxidant levels under OEC photoinactivation (Zhao *et al.* 2021a). Another point worth mentioning is that our data demonstrate AsA can effectively prevent the damage to PSII caused by P_{680}^+, although AsA provides electrons to PSII with a much longer half time than that of OEC (Tóth *et al.* 2009).

In conclusion, the suppression of alternative electron donation was found to damage PSII and there was a decrease in F_v/F_m, an increase in W_K, and disassembly of the PSII RC. This indicates that both AsA and PSII-CEF can assume photoprotective roles. These provide electrons to remit the oxidative stress caused by long-lived P_{680}^+ and thus protect PSII from damage following OEC photoinactivation.

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