

Specific photosynthetic and morphological characteristics allow macroalgae *Gloiopeltis furcata* (Rhodophyta) to survive in unfavorable conditions

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Abstract

Gloiopeltis furcata (Postels & Ruprecht) J. Agardh, a macroalga, which grows in an upper, intertidal zone, can withstand drastic environmental changes caused by the periodic tides. In this study, the photosynthetic and morphological characteristics of *G. furcata* were investigated. The photosynthetic performance and electron flows of the thalli showed significant variations in response to desiccation and salinity compared with the control group. Both PSII and PSI activities declined gradually when the thalli were under stress. However, the electron transport rate of PSI showed still a low value during severe conditions, while the rate of PSII approached zero. Furthermore, PSI activity of the treated thalli recovered faster than PSII after being submerged in seawater. Even though the linear electron flow was inhibited by DCMU [3-(3,4-dichlorophenyl)-1,1-dimethylurea], the cyclic electron flow could still be restored. The rate of cyclic electron flow recovery declined with the increasing time of dark treatment, which suggested that stromal reductants from starch degradation played an important role in the donation of electrons to PSI. This study demonstrated that PSII was more sensitive than PSI to desiccation and salinity in *G. furcata* and that the cyclic electron flow around PSI played a significant physiological role. In addition, *G. furcata* had branches, which were hollow inside and contained considerable quantities of furan. These might be the most important factors in allowing *G. furcata* to adapt to adverse intertidal environments.

Additional key words: cyclic electron flow; desiccation; Dual-PAM; morphology; salinity.

Introduction

G. furcata is an annual red alga of Endocladaceae, Florideophyceae, and it was one of the first artificially cultivated algae in China since the Song Dynasty (Chengkui 1984, Zeng *et al.* 2008). Carbohydrates are the major components of the seaweed, accounting for 56.1% of total dry mass (Tao *et al.* 2001). The polysaccharides of *G. furcata* are known to have antibacterial, antiinflammatory, and antitumor properties (Saeki *et al.* 1996, Park *et al.* 2005, Yu *et al.* 2007, Yu *et al.* 2009). *G. furcata* is important for food, medicine, and textile industries. There

have been attempts to grow the alga using aquaculture techniques.

G. furcata lives higher up the intertidal zone than many other macroalgae, such as *Porphyra* and *Ulva*. Most intertidal macroalgae are submerged in seawater at high tide and exposed to air at low tide, which means that they are severely challenged by the environmental factors, such as high salinity, temperature, and drastic desiccation during low tide (Smith and Berry 1986, Davison and Pearson 1996). The thalli of *G. furcata* have been shown to

Received 19 March 2013, accepted 2 September 2013.

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Abbreviations: AWC – absolute water content; DBMIB – dibromothymoquinone; DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea; ETR – electron transport rate; FNR – ferredoxin-NADP⁺ reductase; F₀ – minimum fluorescence; F_v/F_m – maximum quantum yield of PSII.

Acknowledgments: We thank the reviewers and editors for their sincere working on this manuscript. This research was supported by the nonprofit research project for the State Oceanic Administration (201105008-2, 201105023-7), Strategic Priority Research Program of Chinese Academy of Sciences (XDA11020404) and Strategic Priority Research Program of the Chinese Academy of Sciences (XDA05030401).

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recover rapidly to their normal state after being immersed in seawater. However, the protective and adaptive mechanisms behind the responses of *G. furcata* to environmental stresses are not clear.

Photosynthesis is sensitive to environmental changes and could be one of the important factors determining the impact of stress on algae. Under adverse stress, algae undergo many physiological changes, especially with regards to photosynthesis (Sven and Eshel 1983, Smith *et al.* 1986, Bell 1993, Gao *et al.* 2011). Environmental stresses lead not only to the damage of the photosynthetic apparatus directly, but also affect the activity of enzymes involved in the dark reaction and photosynthetic electron transport (Xu *et al.* 2008, Lin *et al.* 2009, Yang *et al.* 2012). It has been shown that there are two photosynthetic electron transport processes in the thylakoid membrane of the chloroplast: linear and cyclic electron flow. In the linear electron flow, electrons are transferred from water to NADP through 3 major photosynthetic reaction complexes: PSII, cytochrome *b₆f* (cyt *b₆f*), and PSI (Hill and Bendall 1960). In the cyclic electron flow, electrons are recycled from ferredoxin (Fd) or NAD(P)H to plastoquinone (PQ). The cyclic pathway involves PSI,

cyt *b₆f* complex, plastocyanin (PC), and Fd-NADP-reductase (FNR) (Laisk 1993, Joliot and Joliot 2002). To date, the linear electron flow has been intensively investigated. In addition, many reports have shown that cyclic electron flow around PSI plays a significant physiological role in plant responses to stresses, such as desiccation or drought (Bukhov and Carpentier 2004, Gao *et al.* 2011). There have been many studies on electron flows in algae and higher plants undergoing environmental changes (Heber and Walker 1992, Horváth *et al.* 2000, Cruz *et al.* 2001, Gao and Wang 2012). However, the growth environment of higher plants does not change so frequently and dramatically as it does for intertidal algae. Consequently, *G. furcata* represents an excellent material for studying the function of the cyclic electron flow when algae are under stress.

In this study, the photosynthetic performances of PSI and PSII were examined in *G. furcata* in response to severe desiccation and high salinity. The sequential changes in photosynthetic electron transport and photochemical processes subjected to different treatments were recorded and analyzed. The morphological structure and characteristics of the thalli were also studied.

Materials and methods

Sample collection: *G. furcata* thalli were collected from Nanri Island (25°15'29"N, 119°28'26"E), Fujian Province, China. The thalli were rinsed and cleaned in sterilized seawater, then cultured in the laboratory at 10°C with illumination of 100 μmol(photon) m⁻² s⁻¹ in a 12 h dark/12 h light cycle. Healthy thalli in a similar physiological state were chosen for the experiments.

Water content determination: The absolute water content (AWC) of the thalli was determined as follows: $AWC = (M_t - M_d)/(M_0 - M_d) \times 100\%$, where M_d is the mass of the thalli dried at 80°C to constant mass, M_0 is the wet mass of the fresh thalli immediately after removal of water, and M_t is the mass of thalli at time t after dehydration. The thalli were dehydrated naturally at room temperature. At about 8% AWC, the desiccated thalli were put into seawater to rehydrate at room temperature. The photosynthetic properties of the thalli were measured during the dehydration and rehydration processes.

Chlorophyll (Chl) fluorescence and P_{700} measurement:

The Chl fluorescence of PSII and the absorbance changes of PSI were measured at room temperature using a *Dual-PAM-100* (Walz, Effeltrich, Germany) connected to a computer with *WinControl* software. Experiments were carried out using the automated induction and recovery curve routine in the *Dual-PAM* software, with repetitive application of saturation pulses for the assessment of fluorescence and P_{700} parameters. The quantum yields of PSI and PSII were also obtained using the software. In this

study, light from a 620 nm light-emitting diode (LED) and blue actinic light from a 460 nm LED, at a rate of 100 μmol m⁻² s⁻¹, were delivered to the *G. furcata* thalli for 5 min by a *DUAL-DR* measuring. Additionally, saturating light pulses, at a rate of 10,000 μmol m⁻² s⁻¹ and lasting for 300 ms, were also delivered. The *G. furcata* thalli were dark-treated for 10 min before the experiments. First intrinsic fluorescence (F_0) was determined and then a saturating flash was applied to the thalli to detect the maximum fluorescence (F_m). The difference between them is the variable fluorescence (F_v), and the maximum quantum yield is F_v/F_m (Schreiber 2004). Φ_{PSII} is the effective photochemical quantum yield of PSII (Kramer *et al.* 2004). The electron transport rate (ETR) of PSII (ETR_{II}) was calculated using *Dual-PAM* software at the same time as P_{700} was recorded using the dual-wavelength mode of the *Dual-PAM-100* equipment (875 nm and 830 nm pulse-modulated light). Φ_{PSI} and the photosynthetic ETR of PSI (ETR_I) could be also calculated using the *Dual-PAM* software (Pfündel *et al.* 2008).

Salt treatment: *G. furcata* grows on the rocks in the upper, intertidal zone and undergoes severe environmental changes between high tide and low tide. In order to investigate tolerance to salt, the *G. furcata* thalli were incubated at different salinities (15, 30, 45, 60, and 90‰) for 1 h. The thalli were also placed in 90‰ salinity water until ETR_{II} was reduced to zero and then transferred to natural seawater for 30 min. The photosynthetic properties of the thalli in the different environments were measured.

Inhibitor treatments: In order to detect the electron flows around PSI and PSII, *G. furcata* thalli were treated in seawater with the inhibitors, DCMU and dibromothymoquinone (DBMIB), before being measured using a *Dual-PAM-100*. Linear electron flow was reduced or abolished in the presence of DCMU because it blocks electron transport from Q_A in PSII to the mediator, plastoquinone (PQ) (Joët *et al.* 2002). The thalli were treated with 10 μ M DCMU for 5 min and then their physiological state was determined. After measurement, the thalli were treated for another 5 min in the presence of 80 μ M DBMIB. The inhibitor blocks the electron transport from PQ to cyt b_6f complex (Frank and Trebst 1995, Iwai *et al.* 2010), which suppresses effectively the cyclic electron flow around PSI (Herbert *et al.* 1990). The physiological state of the thalli was then measured again. *G. furcata* thalli were also treated with 80 μ M DBMIB alone, in order to observe its influence on the electron flow.

Results

Fluorescence kinetic parameters of thalli during dehydration and rehydration: Both F_v/F_m and F_0 changed during the process of dehydration and rehydration (Fig. 1A,B). F_v/F_m did not change significantly until the AWC reached 35%. It decreased significantly from 27% AWC to 8% (Fig. 1A). F_0 increased before 70% AWC and then declined with further loss of water (Fig. 1B). When the AWC of thalli decreased to about 8%, the thalli were rehydrated. F_v/F_m was fully restored after 20 min (Fig. 1A). After rehydration, F_0 did not change substantially compared to 100% AWC (Fig. 1B).

ETRI and ETRII during desiccation and rehydration: The ETR of PSI and PSII changed during desiccation and rehydration (Fig. 1C). The ETRII decreased steadily in dependence of AWC and it reached zero at 13% AWC. There were no significant changes in ETRI from 100% AWC to 35%. Subsequently, ETRI declined significantly and dropped to zero when AWC reached 8%. After 5-min rehydration, ETRI recovered rapidly to a level similar to fully hydrated thalli (100% AWC). However, ETRI showed a small reduction after a further period of rehydration. ETRII also rose significantly during the rehydration but did not reach the rate observed before dehydration.

F_v/F_m and ETR of the thalli when responding to salinity: There were no significant differences in F_v/F_m in the thalli after being treated with various salt concentrations except for 90‰ for 1 h (Fig. 2A). ETRI and ETRII decreased gradually as the salinity rose (Fig. 2B).

In addition, the thalli were immersed in 90‰ salinity for different periods of time. F_v/F_m decreased as the treatment duration increased (Fig. 3A). There were significant changes between the beginning of dehydration and after

Dark treatment: In order to study the influence of starch degradation on photosynthetic electron flow, the *G. furcata* thalli were incubated in the dark at 20°C for 12, 24, 48, and 72 h. After the dark treatment, the thalli were immediately treated with 10 μ M DCMU in the dark for 5 min. Then the thalli were dehydrated naturally in the presence of DCMU to avoid the effect of linear electron flow on cyclic electron flow around PSI. When AWC reached about 8%, the thalli were rehydrated in seawater containing 10 μ M DCMU for 5 min. The photosynthetic properties of the thalli were then measured.

Statistical analysis: The results were expressed as mean values \pm standard deviation (SD). Data were analyzed using *SPSS 18.0* (SPSS Inc., Chicago, USA) statistical software by analysis of variance (ANOVA). When the $P \leq 0.05$ significance level was achieved, Tukey's multiple comparison test was used to determine any significant differences between the different treatments.

1 h. The thalli treated for 28 h were allowed to recover in natural seawater for 30 min. The F_v/F_m rose to a level approached under the normal state of the thalli. Simultaneously, as the treatment duration increased, ETRII declined and dropped to zero after 28 h. ETRI also decreased as the treatment duration increased but when ETRII dropped to zero, ETRI was still high. During the recovery period, both ETRI and ETRII showed large, significant enhancement compared with the state after 28 h of treatment (Fig. 3B).

ETRI and ETRII in response to inhibitors: When thalli were treated with DCMU, ETRII dropped directly to zero, which meant that linear electron flow was inhibited (Fig. 4A). ETRI decreased significantly to a low rate, but there were no significant differences compared to the further treatment with DBMIB. When the thalli were treated only with DBMIB, ETRII also dropped to zero while ETRI decreased significantly to a low rate (Fig. 4A). This suggested that the inhibitor, DBMIB, penetrated the cell but did not completely suppress the cyclic electron flow. The main reason for this might be that DBMIB can bypass its own block, which means that DBMIB is hydrophilic enough to enter the lumen and donate electrons (though slowly) to either PC or P700 (Schansker *et al.* 2005).

ETRI in response to varying duration of dark treatment: When the AWC of the thalli reached about 8%, both ETRI and ETRII dropped to zero, but recovered rapidly during rehydration (Fig. 1C). In addition, when DCMU was present, PSI activity of the desiccated thalli at 8% AWC could still be restored (Fig. 4B). This indicated that the cyclic electron flow around PSI could recover during rehydration, even though the linear electron flow was inhibited.

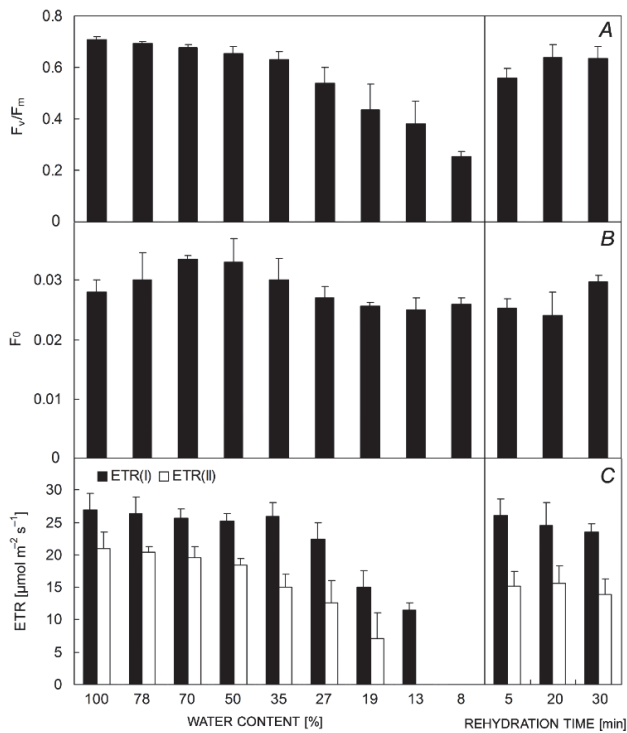


Fig. 1. Variations of *Gloiopeltis furcata* thalli parameters during desiccation and rehydration. Means \pm SD, $n = 5$. A: maximum quantum yield of PSII (F_v/F_m); B: minimum fluorescence (F_0); C: electron transport rate (ETR).

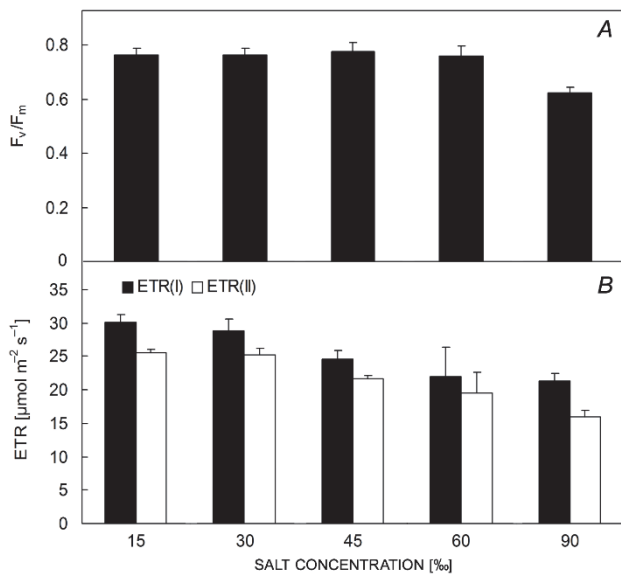


Fig. 2. Changes of A: maximum quantum yield of PSII (F_v/F_m) and B: electron transport rate (ETR) in *Gloiopeltis furcata* at different salinities after 1 h. Means \pm SD, $n = 5$.

Bukhov *et al.* (2002) suggested that starch degradation may provide exogenous NAD(P)H and electrons to the intersystem electron carriers. The dark-treatment experiments were undertaken in order to study the influence of

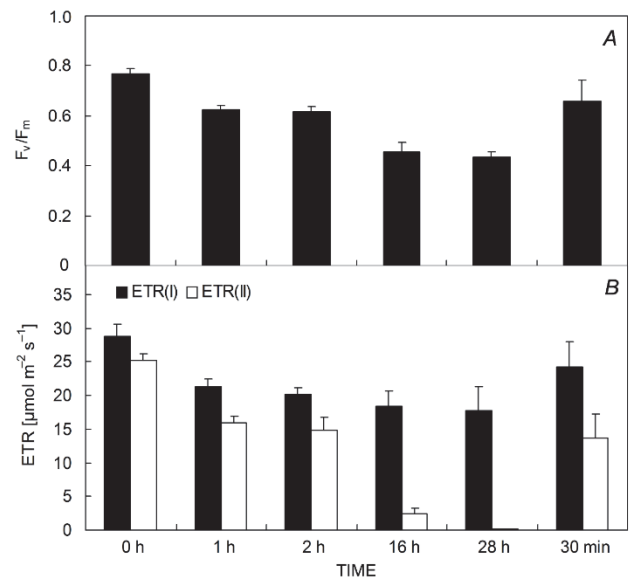


Fig. 3. Changes of A: maximum quantum yield of PSII (F_v/F_m) and B: electron transport rate (ETR) in *Gloiopeltis furcata* in 90‰ salinity for different periods of time. The last line means that the thalli, treated for 28 h, were transferred to nature seawater for 30 min. Means \pm SD, $n = 5$.

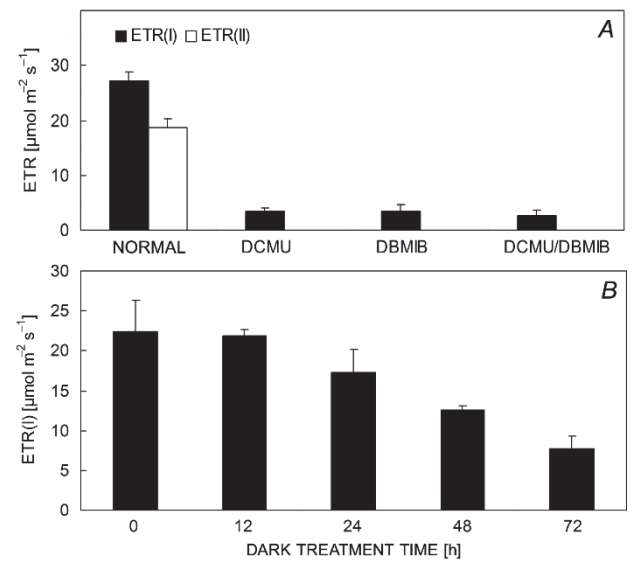


Fig. 4. A: electron transport rates of PSI (ETRI) and PSII (ETRII) of *Gloiopeltis furcata* responses to DCMU (10 μM) and DBMIB (80 μM). B: The influence of dark treatment on the recovery of cyclic electron flow around PSI in desiccated thalli (8% absolute water content). The desiccated thalli were rehydrated in the presence of DCMU. Means \pm SD, $n = 5$.

starch degradation on the cyclic electron flow recovery. At 8% AWC, the desiccated thalli were rehydrated in the presence of DCMU. The ETRI decreased gradually as the dark-treatment period increased (Fig. 4B). The electron flow rate of the thalli after 72 h of darkness was much lower compared with nontreated thalli.

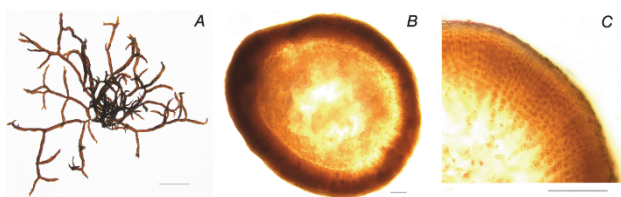


Fig. 5. Internal structure of the *Gloiopeltis furcata*. A: wild thalli; B: thalli cross section; C: part of the cross section. Bar – 1 cm (A), 100 μm (B,C).

Discussion

The morphological characteristics of *G. furcata* is helpful to resist stress: F_v/F_m is a sensitive indicator of the photosynthetic activity of plants and decreases when plants are subjected to stress, such as high temperature, dehydration, high salt, *etc.* (Maxwell and Johnson 2000). In this study, the F_v/F_m decreased in *G. furcata* thalli similarly as in higher plants when responding to desiccation. However, the decrease of F_v/F_m was not significantly different at the onset of the desiccation stage compared to that before dehydration and the thalli could recover rapidly when emerged in seawater, even though they had lost more than 90% of their internal water (Fig. 1). In higher plants, the inactivation of PSII due to photoinhibition or a loss of Mn-cluster caused by heat stress (Aro *et al.* 1993, Tóth *et al.* 2005) leads to the degradation, repair, and reassembly of PSII, a process taking several hours. On the other hand, the desiccation in lichen leads to an inactive state of PSII that can be quickly (within min) reversed by the addition of water (Heber *et al.* 2011, Oukarroum *et al.* 2012). In this respect, *G. furcata* behaved more like lichen.

Compared to *Ulva* sp. and *Porphyra yezoensis* (Gao *et al.* 2011, Gao and Wang 2012), the changes of F_v/F_m were not large in *G. furcata* thalli responding to desiccation. Gao and Wang (2012) reported that F_v/F_m decreased significantly as water loss increased in *P. yezoensis* blades. However, in *G. furcata*, there were no significant changes found until the AWC reached 35% (Fig. 1A), which suggested that *G. furcata* had a stronger tolerance to desiccation. *G. furcata* has multilayered, cellular structures and the branches are hollow inside (Fig. 5), whereas *P. yezoensis* blades are composed of a cell monolayer. Some free water might remain in the *G. furcata* cavities, even though the seawater was removed at the beginning of the experiment. Furthermore, the thalli contained high contents of funoran, which is composed of the repeated units of β -D-galactose and 3,6-anhydro- α -L-galactose. It behaves like agar (Hirase *et al.* 1958, Hirase and Watanabe 1972). Agar has a special trait – syneresis, which enables agar gel to secrete water in the surface (Hayashi and Okazaki 1970). This feature seemed to help *G. furcata* withstand adverse circumstances.

There was a transitory increase in F_0 during desiccation

The morphological structures and characteristics: *G. furcata* thalli had irregular, cylindrical branches (Fig. 5A). The cross section showed that the thalli were hollow inside and full of funoran (Fig. 5B). Furthermore, the thalli seemed to be composed of multiple layers of cells (Fig. 5C).

of the thalli, but it decreased subsequently after further desiccation (Fig. 1B). It has been proposed that the increase of F_0 was caused by the separation of light-harvesting pigment protein complex from the PSII core complexes in the isolated chloroplasts under heat-induced conditions (Schreiber and Armond 1978). In addition, Yamane *et al.* (1997) thought that the cause of the increase in the F_0 level was not only the separation of the LHCII from the PSII core complexes, but also a partly reversible inactivation of the PSII reaction center. Based on these reports, we tentatively suggested that both the reversible inactivation of the PSII reaction center and the separation of LHCII from the PSII core complexes might cause the transient increase of F_0 in epidermal cells during the initial desiccation phase. Following further dehydration, funoran might provide water to epidermal cells to support photosynthesis. This was another aspect that demonstrated that the morphology and structural components helped *G. furcata* tolerate desiccation.

The salinity of *G. furcata* thalli increased as they dehydrated. F_v/F_m was still high (~ 0.4) in adverse conditions of being exposed to 90‰ salinity for 28 h. *G. furcata* showed the strong tolerance to salinity as well as to dehydration. The reasons for such high salinity tolerance were probably similar to the reasons behind the high tolerance to desiccation (Figs. 2,3).

PSII is more sensitive than PSI to desiccation and salinity: The PSI activity decreased gradually during the process of desiccation and until it reached a rate of about 12 μmol (photon) $\text{m}^{-2} \text{s}^{-1}$ at 13% AWC, where the linear electron flow had stopped (Fig. 1C). When treated in 90‰ saline water for 28 h, ETRII dropped to zero while ETRI still had a value of about 17 μmol (photon) $\text{m}^{-2} \text{s}^{-1}$ (Fig. 3B). This showed that PSI-driven, cyclic electron flow in *G. furcata* thalli was still active under severe environmental stress, even though the linear electron flow stopped. These results implied that PSII was more sensitive than PSI in responding to desiccation and salinity. In addition, the photosynthetic parameters of the thalli showed a significant recovery within minutes following rehydration. The PSI activity rose rapidly to the same level as in the nonstressed thalli, while PSII still showed significant differences compared with the nonstressed state. This was similar to the

photosynthetic performance pattern in *Porphyra katadai* and *P. yezoensis* when subjected to desiccation (Lin *et al.* 2009, Gao and Wang 2012).

Exogenous electrons were donated to PSI: After the thalli were treated with DCMU, ETRII quickly dropped to zero, while ETRI decreased to a low rate but it was still functioning to some degree (Fig. 4A). It suggested that the electrons removed from water were donated to PSI. Furthermore, when the thalli were treated with DCMU at 8% AWC, where both ETRI and ETRII decreased to zero, ETRI could be restored to more than 20 $\mu\text{mol (photon)} \text{ m}^{-2} \text{ s}^{-1}$ (Fig. 4B). The ETRI value was higher than that of the thalli treated with DCMU directly, which suggested that there might be other sources of electrons for PSI during desiccation. The electrons from cellular metabolism may have a positive effect on PSI. It was reported that exogenous NAD(P)H could donate electrons to inter-system electron carriers (Bukhov *et al.* 2002, Bukhov and Carpentier 2004). Murthy *et al.* (1988) reported that amylase activities showed a significant increase during the first 2 h of the desiccation process in *Ulva lactuca* from upper tidal zone, which might influence photosynthesis. In addition, the biological process of starch breakdown played an important role in the donation of electrons to photosynthetic cyclic electron flow in *Chlamydomonas reinhardtii* (Johnson and Alric 2012). In this study, the

dark treatment showed that ETRI decreased gradually as treatment duration increased when the thalli were rehydrated in DCMU at 8% AWC (Fig. 4B). The result suggested that starch degradation caused a decline in the pool of stromal reductants, including NAD(P)H, which donated electrons to PSI and influenced the restoration of cyclic electron flow in desiccated *G. furcata* during rehydration. This could be one of the main reasons why PSI was less sensitive to stress (*e.g.*, desiccation and salinity) than PSII.

Besides major photosynthetic complexes of oxygenic photosynthesis (the so-called 'Z' scheme), chlororespiration is also proposed based on electron transfer reactions from stromal reductants to O₂ through PQ pool (Bennoun 1982, Peltier and Cournac 2002, Bukhov and Carpentier 2004). These components include a plastid NAD(P)H dehydrogenase (NDH) complex and a plastid terminal plastoquinone oxidase (PTOX). The existence of the complex network regulating expression and activity of the NDH complex and PTOX in response to environmental stress indicates that these components likely play a role in the acclimation of photosynthesis to changing environmental conditions. In response to severe stress conditions, PTOX associated to the NDH and/or the proton gradient regulation 5 (PGR5) pathway may also limit electron pressure on PSI acceptor and prevent PSI photoinhibition (Rumeau *et al.* 2007).

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