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Photosynthetic responses of the low intertidal macroalga *Sargassum fusiforme* (Sargassaceae) to saline stress

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Abstract

Sargassum fusiforme, a species of brown seaweed with economic importance, inhabits lower intertidal zones where algae are often exposed to various stresses. In this study, changes in the photosynthetic performance of *S. fusiforme* under saline stress were investigated. The PSII performance in *S. fusiforme* significantly improved, when the thalli were exposed to 0% salinity, and remained high with prolonging treatment time. In contrast, the PSII activity declined considerably under salinities of 4.5 and 6%. The PSI activity did not change remarkably under saline stress, thus demonstrating higher tolerance to saline stress than PSII. In addition, the PSI activity could be also restored after saline treatments, when PSII was inhibited by 3-(3,4-dichlorophenyl)-1,1-dimethylurea. It might be as a result of changes in the NAD(P)H content in the thalli under saline stress. Our results suggested that PSI was much more tolerant to different saline stress than PSII in *S. fusiforme.* We demonstrated that *S. fusiforme* was much more tolerant to hyposaline than to hypersaline stress.

Additional key words: chlorophyll fluorescence; chrysolaminarin; electron transport rate; nonphotochemical quenching; reductant.

Introduction

Sargassum fusiforme (Sargassaceae) is considered to be a synonym of *Hizikia fusiformis* (Stiger *et al*. 2003, Zou *et al*. 2012), which is a commercially important brown alga cultivated intensively in China, especially in Zhejiang and Fujian provinces (Pang *et al*. 2008). It is an edible alga and is the raw material for alginate production (Zou and Gao 2010). Moreover, it has been reported that the large scale aquaculture of *S. fusiforme* could alleviate eutrophication through the uptake of nutrients (Zou 2005). Due to its high commercial value and ecological significance, a large number of studies have been undertaken and mainly focused on the cultivation, seeding and life history of *S. fusiforme* (Hwang *et al*. 1997, Pang *et al*. 2005, Zou *et al*. 2006). However, there have been very few studies on tolerance and responses of *S. fusiforme* to stresses.

Sargassum fusiforme is a representative species of intertidal brown macroalga, which inhabits the lower intertidal zones of rocky shores (Tseng 2000). During low tides, especially very low tides, the thalli experience a variety of stresses, such as high irradiance and hypersaline stress. At low tide, particularly, during the day, ambient sea water surrounding *S. fusiforme* thalli evaporates and the salinity increases, which results in the thalli being subject to hypersaline stress frequently, especially during the summer. Additionally, *S. fusiforme* frequently experiences also hyposaline conditions due to the fact that thalli are frequently immersed in fresh water during rains. Moreover, the tolerance of *S. fusiforme* to hyposaline stress has

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Abbreviations: DCMU – 3-(3,4-dichlorophenyl)-1,1-dimethylurea; ETR – electron transport rate; $ETR_{II\ (I)}$ – relative rate of electron transport in PSII (PSI); FM – fresh mass; F_v/F_m – maximal quantum yield of PSII photochemistry; NPQ – nonphotochemical quenching; P_0 – zero P700 signal; P_m – maximal P700 signal, S0 – fresh water; S1.5 – 1.5% salinity; S4.5 – 4.5% salinty; S6 – 6% salinity; SWC – normal, control sea water; Y(I) – the effective photochemical quantum yield of PSI.
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been employed in *S. fusiforme* aquaculture. Nets of *S. fusiforme* are immersed in fresh water by farmers for several hours to remove harmful epiphytic algae from *S. fusiforme* thalli. To date, although the effects of saline stress have been documented on photosynthetic processes in plants and green algae (Allakhverdiev *et al*. 2000, Chen *et al*. 2011, Azzabi *et al*. 2012, Liu *et al*. 2012), there is little information available on response mechanisms to saline stress in *S. fusiforme*.

Physiological responses and tolerance mechanisms of *S. fusiforme* to saline stress were investigated in this study. Furthermore, particular attention was paid to the changes in the PSI and PSII activities during saline stress and recovery.

Materials and methods

Sample collection: *Sargassum fusiforme* (Sargassaceae) thalli were collected from the shores of Wenzhou (27°29'35"N, 121°05'24"E), China. The thalli were rinsed in sterile sea water to remove any sediment or epiphytes and then they were cultured in the laboratory at 20°C and under the irradiance of 150–160 μmol(photon) m^{-2} s^{-1}. Healthy thalli in a similar physiological state were selected for further investigation.

Saline-stress treatment: In this study, normal sea water (3% salinity) was used as a control (SWC). A salinity of 0% (S0) was obtained using fresh water (distilled water from the lab), and 1.5% salinity (S1.5) was achieved by diluting the control with fresh water. The higher salinities (4.5 and 6%, S4.5 and S6, respectively) were obtained by adding crude salt to normal sea water and determining the salinity with a salinometer (*IS/Mill-E*, *ASONE*, Japan). *S. fusiforme* thalli were immersed in the different saline solutions for 2 h. During treatments, the photosynthetic activities of the thalli were measured after 30, 60, 90, and 120 min. After each treatment, the thalli were allowed to recover for 5 min in normal sea water and then the photosynthetic activity was measured again. In addition, the thalli treated with the different saline solutions were rehydrated in sea water with different concentrations (5 and 10 μM) of 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU), an efficient inhibitor of PSII, for 5 min in darkness. The photosynthetic activity of the thalli was then measured. During the saline-stress treatment, the irradiance was 150–200 μmol(photon) m^{-2} s^{-1}.

Chlorophyll (Chl) fluorescence and P700 measurement: The photosynthetic activities of the thalli were measured during the saline-stress treatment using a *Dual-PAM-100* fluorometer (*Walz*, Effeltrich, Germany). Before measurement, the thalli were dark-adapted for 5 min. The minimum fluorescence (F_0) was determined and a saturating flash was subsequently applied to detect the maximal fluorescence (F_m). The difference between F_m and F_0 is the variable fluorescence (F_v) and F_v/F_m is the maximum quantum yield. The relative rate of electron transport in PSII (ETR_{II}) was calculated by *Dual-PAM* software, which represents the efficiency of PSII photochemistry achieved under illumination. Nonphotochemical quenching (NPQ) was calculated as $(F_m - F_m')/F_m'$ (Genty *et al*. 1989). In this study, the actinic illumination from 635 nm LED arrays was 130 μmol(photon) m^{-2} s^{-1}. Additionally, saturating light pulses of 10,000 μmol(photon) m^{-2} s^{-1} and 300 ms duration were delivered.

P700 was measured in the dual-wavelength mode (a difference between the intensities of 875 and 830 nm pulse-modulated light reaching a photodetector). The maximal P700 signal, P_m, was determined by applying the saturation pulse in the presence of far-red light, which was defined similarly as F_m. The saturation light pulse from 635 nm LED arrays was 10,000 μmol(photon) m^{-2} s^{-1} and the duration time was 10 ms. The zero P700 signal, P_0, was determined when complete reduction of P700 was induced after the saturation pulse and cessation of far-red illumination. P_m' is the maximal P700 signal induced by combined actinic illumination plus the saturation flash (Klughammer and Schreiber 1994). Y(I) is the effective photochemical quantum yield of PSI. The relative rate of electron transport rate in PSI (ETR_I) was calculated by *Dual-PAM* software (Klughammer and Schreiber 2008).

Determination of NADPH and NADH: *S. fusiforme* thalli were treated with the different saline solutions (S0, S1.5, S4.5, and S6, respectively) for 2 h under the irradiance of 130 μmol(photon) m^{-2} s^{-1}. The control was immersed in sea water for the same time period. After treatment, the NADPH and NADH contents were determined according to Matsumura and Miyachi (1983). An equal amounts of the thalli fresh mass (FM) were grinded and then transferred to NaOH (0.1 M). The suspensions were kept at 100°C for 2 min, then cooled to 0°C and centrifuged (10,000 × *g* at 4°C). NADPH and NADH were specifically extracted in the supernatant obtained after the alkaline treatment. The alkaline extract was neutralized by adding an equivalent amount of HCl, followed by addition of 0.1 ml of EDTA (40 mM), 3-(4,5-dimethylthiazolyl-2)-2,5-diphenyltetrazolium (MTT) (4.2 mM), phenazine ethosulfate (PES) (16.6 mM), and ethanol for the determination of NADH, or 0.05 ml of glucose-6-phosphate (G6P) for the determination of NADPH. After adjusting the total volume to 1 ml by adding H_2O, the test tubes were kept at 37°C for 5 min. The reaction was started by adding 0.02 ml of alcohol dehydrogenase (for NADH) or G6P dehydrogenase (for NADPH). After a proper reaction time (30–60 min), the absorbance at 570 nm was determined by spectrophotometer (*UV1800, Shimadzu*, Japan).

Measurement of soluble sugar and chrysolaminarin: In order to investigate the response of storage carbohydrates in brown algae to saline stresses, the content of soluble sugars and chrysolaminarin in the *S. fusiforme* thalli treated with different salinities (0, 1.5, 4.5, 6%, and control) were determined according to the methods described by Beattie *et al*. (1961), Sánchez *et al*. (1998), and Brányiková *et al*. (2011). The samples of equal FM were frozen in liquid nitrogen, ground into a powder, and then dried at 105°C to a constant mass. Soluble sugars were extracted using 8 ml of 80% ethanol at 68°C for 15 min and centrifuged (10,000× *g* for 10 min). This step was repeated three times. The supernatants were combined and volatilized at 85°C in a water bath to a volume of 2–3 ml. Distilled water was then added to make a final total volume of 10 ml. For the total hydrolysis of chrysolaminarin, 3.3 ml of 30% perchloric acid were added to the sediment, stirred for 15 min, and centrifuged. This procedure was repeated three times. The extracts were combined and distilled water was added to make a final volume of 10 ml (Beattie *et al*. 1961, Brányiková *et al*. 2011). Then, 0.1 ml of the soluble sugar and 0.1 ml of the chrysolaminarin extracts were cooled to 0°C, after which 1 ml of anthrone solution [2 g of anthrone in 1 l of 72% (v/v) H_2SO_4] was added and rapidly blended. The mixtures were kept in a water bath at 100°C for 8 min. They were then cooled to 20°C and the absorbance was measured at 625 nm (*UV1800, Shimadzu*, Japan). A standard curve was created using glucose. The soluble sugar contents were determined according to the calibration curve and the chrysolaminarin contents were obtained by multiplying the measured values by 0.9.

Statistical analysis: The results were expressed as mean values of five independent experiments ± standard deviation (SD). Data were used for statistical analysis *via* one-way analysis of variance (*ANOVA*) using the *SPSS 18.0* statistical software. For *post-hoc* analysis, the *Tukey*'s test was used at $\alpha = 0.05$ significance level.

Results

Effects of hypo- and hypersaline stress on the photosynthetic activities of *S. fusiforme*: The photosynthetic performance of *S. fusiforme* thalli varied under hypo- and hypersaline stress (Fig. 1). During hyposaline stress treatment (S0 and S1.5), there was no significant change in F_v/F_m. In contrast, F_v/F_m decreased significantly during the hypersaline stress treatment (S4.5 and S6), which indicated that the thalli were experiencing stress. The F_v/F_m values of the thalli treated with all hyposaline and hypersaline solutions were restored to their pretreatment levels after 5 min of recovery (Fig. 1). During saline stress, ETR_{II} also changed considerably (Fig. 2*A*), increasing significantly after 30 min of freshwater treatment (S0) and remaining at this higher level for up to 120 min, but decreased to a level prior the treatment when the thalli were rehydrated with sea water. There was also a slight increase in ETR_{II} during the S1.5 treatment. In contrast, high salinities caused a reduction in ETR_{II}. Moreover, hypersaline stress also resulted in a change of ETR_I; it decreased significantly during the S6 treatment. During recovery, the photosynthetic activity of the thalli subjected to hypo- and hypersaline stress was almost completely restored to levels prior the treatment. All results demonstrated that the hyposaline treatments did not negatively affect the photosynthetic activity of *S. fusiforme* thalli. The photosynthetic activity even increased under freshwater treatment. This suggested that the thalli adapted well to hyposaline conditions.

We also observed that hypo- and hypersaline stress strongly affected NPQ in *S. fusiforme* thalli (Fig. 3). The NPQ in thalli subjected to the S1.5 treatment was much

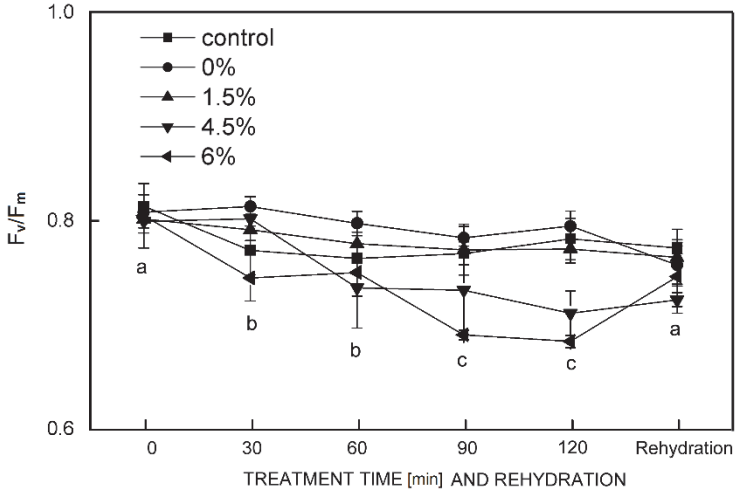

Fig. 1. Variations in F_v/F_m of *Sargassum fusiforme* during the course of different saline treatments (0, 1.5, 4.5, 6%, and control) and rehydration in normal sea water. Data show the means of five independent experiments (± SD). *Different letters* represent significant differences between the duration of the treatment with 6% salinity, respectively ($p<0.05$, *ANOVA*, followed by *Tukey*'s *post-hoc* test for comparisons).

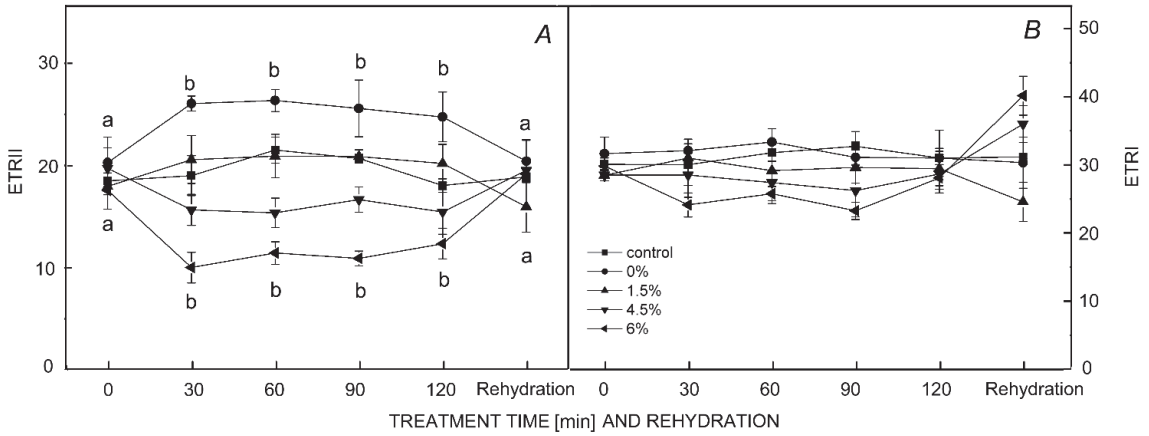

Fig. 2. Changes in ETR_{II} (*A*) and ETR_I (*B*) of *Sargassum fusiforme* during the course of different saline treatments (0, 1.5, 4.5, 6%, and control) and rehydration in the normal sea water. Data show the means of five independent experiments (± SD). In *A*, *different letters* represent significant differences between the duration of the treatments with 4.5 and 6% salinity, respectively (p<0.05, *ANOVA*, followed by *Tukey*'s *post-hoc* test for comparisons).

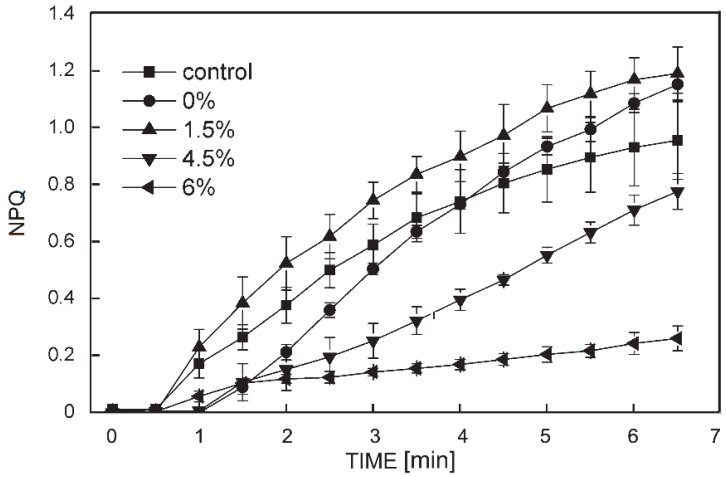

Fig. 3. Nonphotochemical quenching (NPQ) in *Sargassum fusiforme* was measured after 120 min of treatment with different salinities (0, 1.5, 4.5, 6%, and control). Data show the means of five independent experiments (± SD).

higher than that of the SWC thalli. The freshwater treatment also induced a significant increase in NPQ compared to the SWC thalli. NPQ decreased significantly after the high salinity (S4.5 and S6) treatments, especially, after the S6 treatment, where NPQ declined to a very low level. These results suggested that hyposaline stress could increase the NPQ capacity in *S. fusiforme* thalli, which might help protect the photosynthetic apparatus at low salinities. However, NPQ in the thalli was negatively affected by higher salinities.

***S. fusiforme* thalli response to DCMU during saline stress**: After 120 min of the salinity treatments, the thalli were rehydrated in sea water containing DCMU in order to investigate PSI recovery when PSII was inhibited by DCMU. Interestingly, when the thalli were rehydrated with 10 μM DCMU. According to the ETR_I and ETR_{II} values (Fig. 4*A*), neither PSI nor PSII could be restored. When the thalli were rehydrated with 5 μM DCMU, PSII was inhibited and PSI decreased to a lower level than that in the control thalli. Moreover, during rehydration in sea water containing 5 μM DCMU, the thalli exposed to S6 showed a higher PSI activity than that of the control. It was also clear that the ETR_I values during the recovery were lower than those measured in the thalli without DCMU during saline stress. Furthermore, there were significant differences between the untreated and the DCMU-treated thalli during saline stress (Fig. 4*C*). This result suggested that the activity of PSII during saline stress strongly affected the recovery of PSI during the recovery stage.

Changes in reductant, soluble sugar, and chrysolaminarin contents: Hyper- and hyposaline stress had different effects on reductant, soluble sugar, and chrysolaminarin contents (Fig. 5). The reductant contents (NADPH and NADH) increased significantly, compared with the control,

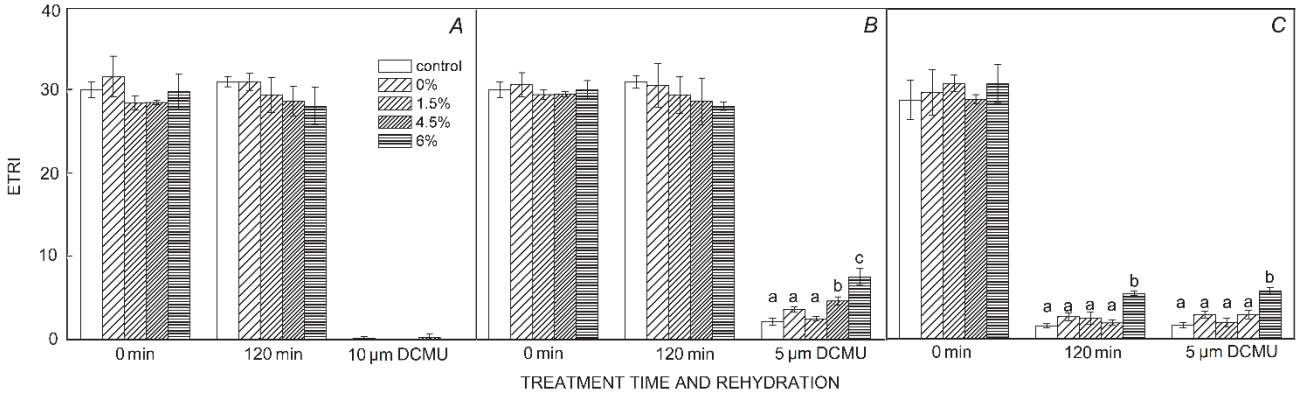

Fig. 4. After 120 min of treatment with different salinities (0, 1.5, 4.5, 6%, and control), the *Sargassum fusiforme* thalli were rehydrated for 5 min in sea water containing 10 μM DCMU (*A*) and 5 μM DCMU (*B*) prior to measurement of electron transport through PSI (ETR_I). After 120 min of treatment with different salinities containing 5 μM DCMU (to inhibit PSII), the thalli were rehydrated for 5 min in sea water containing 5 μM DCMU prior to measurement of ETR_I (*C*). Data show the means of five independent experiments (± SD).

after the thalli were subjected to hypersaline stress. The NADPH and NADH contents decreased considerably after the S1.5 treatment. In contrast, there was a slight increase in the NADPH contents of the thalli treated with fresh water. Therefore, we determined the soluble sugar and chrysolaminarin contents after 120 min under saline stress. The results suggested that after being subjected to the hypersaline treatments for 120 min, the chrysolaminarin content in the thalli was much lower than that in SWC. However, there was no significant difference between the thalli treated with fresh water and SWC. After 120 min of the hyposaline treatment, the soluble sugar content did not change significantly in comparison with SWC. The soluble sugar content in the thalli subjected to hypersaline stress decreased significantly. All these results suggested that the different salinity treatments affected significantly chrysolaminarin and soluble sugar metabolism in *S. fusiforme* thalli.

Discussion

In plants and algae, photosynthesis is not only an essential process, which converts light energy to chemical energy, but acts also as an environmental sensor that can be significantly affected by many different stresses (Pfannschmidt 2003, Bräutigam *et al*. 2009). The PAM measuring system is convenient and nonintrusive and has been proven as a useful tool for assessing physiological states of higher plants and green algae (Huang *et al*. 2010, Johnson and Ruban 2010, Gao *et al*. 2011). In fact, PAM has been also used for examination of photosynthesis in brown or red algae and has provided many valuable and interesting results (Harker *et al*. 1999, Aguilera *et al*. 2002, Pang *et al*. 2007). The photosynthetic parameter, F_v/F_m, is a sensitive indicator of photosynthetic performance and declines significantly when plants experience stresses (Maxwell and Johnson 2000). We observed that the F_v/F_m of *S. fusiforme* decreased under the hypersaline treatment; it could be restored rapidly to normal level after 5 min of recovery in sea water. Moreover, the F_v/F_m ratio was hardly affected by hyposaline stress (S0). These results suggested that *S. fusiforme* demonstrated higher tolerance to hyposaline than to hypersaline stress. In fact, the photosynthetic activities of *S. fusiforme* could remain nearly constant over a wide temperature range (Zou and Gao 2005). *Sargassum fusiforme* could also withstand high-light stress and the photosynthetic activity could maintain a constant rate (Pang *et al*. 2007). Moreover, the photosynthetic acclimation to low-light conditions could be rapidly achieved in *S. fusiforme* (Zou and Gao 2010). Published data, together with our results, suggested that alike higher intertidal macroalgae, *S. fusiforme* also demonstrated more tolerance to a variety of stresses including saline stress, temperature, and high-light stress, although it inhabits low intertidal zones.

We further observed that during the saline treatment, PSI and PSII in *S. fusiforme* showed different responses to the saline stress. PSI in *S. fusiforme* demonstrated higher tolerance to saline stress than PSII. It has been reported that in higher plants, green macroalgae, and red macoralgae, PSI shows a higher tolerance to low temperature, desiccation or osmotic stress (Golding and Johnson 2003, Huang *et al*. 2010, Gao *et al*. 2011, 2014). These studies suggested that under stress conditions, linear electron flow decreased and cyclic electron flow around PSI was activated, which plays an important role in stress tolerance of plants (Golding and Johnson 2003, Gao and Wang 2012). Our results suggested that during hypersaline stress, the PSII activity decreased remarkably and the activity of PSI did not change. It is possible that in *S. fusiforme* linear electron flow was downregulated and

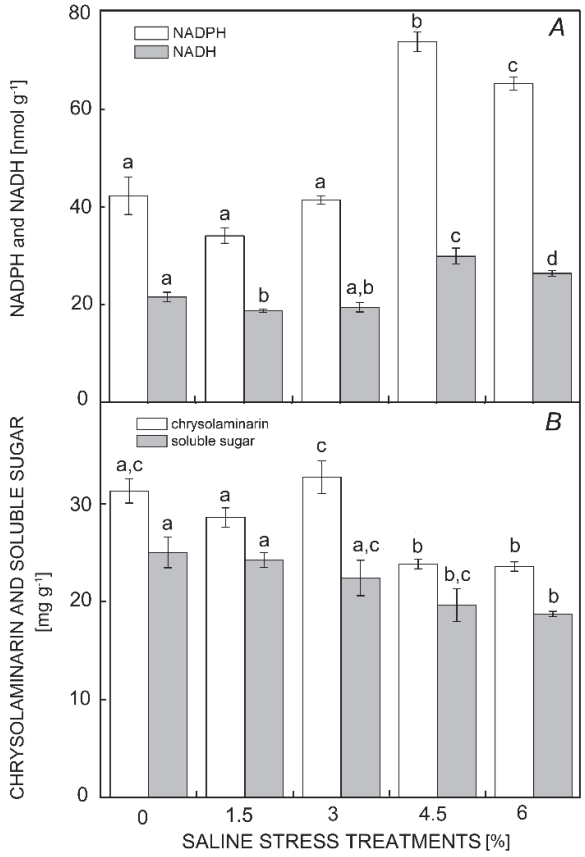

Fig. 5. The content of NADPH and NADH (*A*) and chrysolaminarin and soluble sugar content (*B*) in the *Sargassum fusiforme* thalli treated with different saline solutions for 120 min. The nmol g^{-1} in (*A*) represents the amount per gram of fresh thalli. The mg g^{-1} in (*B*) represents the amount per gram of fresh thalli. Data show the means of five independent experiments (± SD). *Different letters* represent significant differences between different salinities ($p<0.05$, *ANOVA*, followed by *Tukey*'s *post-hoc* test for comparisons).

cyclic electron flow was activated under hypersaline stress. During the recovery, whereas PSII was inhibited, the PSI activity in *S. fusiforme* could still be restored, suggesting that the recovery of the cyclic electron flow around PSI could be independent of the linear electron flow. In fact, many reports have proposed that NADPH and NADH derived from starch degradation can donate electrons to intersystem electron carriers and affect cyclic electron flow around PSI (Bukhov and Carpentier 2004, Alric 2010, Johnson and Alric 2012, Gao *et al*. 2013). Our previous study has demonstrated that NADPH in gren algae increased under hyperosmotic stress and played an important role in the recovery of the cyclic eletron flow around PSI (Gao *et al*. 2014). The present results suggested that the content of NAPDH in *S. fusiforme* increased significantly under hypersaline stress, which is consistent with the PSI activity during recovery as PSII was inhibited. It is known that brown algae use chrysolaminarin as storage carbohydrate (Beattie *et al*. 1961). The degradation of chrysolaminarin in *S. fusiforme* occurred under hypersaline stress. However, the soluble sugar content in the thalli subjected to higher salinities was slightly lower than that in the control (Fig. 5*B*). Actually, during the course of hypersaline stress, *S. fusiforme* thalli released light yellow and soluble solutions, which were composed of fucose and ribose (unpublished data). It was proposed that the release of carbohydrates caused a decrease in the soluble sugar content of the thalli subjected to hypersaline stress. This special response mechanism of *S. fusiforme* thalli to hypersaline stress was different from that of green algae (Huan *et al*. 2014).

Overall, PSI in *S. fusiforme* showed a higher tolerance to saline stress than PSII, and the recovery of PSI could be independent of the linear electron flow and might be affected by the content of NADPH in the thalli.

Saline stress has also significant effects on NPQ in *S. fusiforme* thalli. NPQ is one of the mechanisms which contribute to suppression of reactive oxygen species (ROS) generation and it also plays an important role in photoprotection (Niyogi and Truong 2013). Moreover, NPQ is regulated by environmental stress, especially, by irradiance conditions (Murchie and Niyogi 2011, Tokutsu and Minagawa 2013). It has been reported that both hypo- and hypersaline stress can enhance the generation of ROS (Dring 2005, Parida and Das 2005, Liu *et al*. 2012). Our results suggested that hyposaline stress induced a significant increase in NPQ in comparison with the control. Therefore, it is possible that under hyposaline conditions, *S. fusiforme* thalli were able to prevent ROS formation by increasing NPQ. However, a significant decrease in NPQ occurred in the thalli subjected to the higher salinity. In contrast, moderate hyperosmotic conditions induced by sodium chloride and sorbitol could enhance NPQ in moss and green algae (Azzabi *et al*. 2012, Gao *et al*. 2014). This special response of NPQ in *S. fusiforme* to hypersaline stress demonstrated that there might be a particular tolerance mechanism in *S. fusiforme* to hypersaline stress.

PSI in *S. fusiforme* demonstrated much higher tolerance, which could still be restored even if PSII was inhibited. This suggested that the cyclic electron flow around PSI plays an important role during recovery, which might be correlated with the content of NAPDH in the thalli. Moreover, *S. fusiforme* demonstrated much higher tolerance to hyposaline stress than to hypersaline stress. These special responses to saline stress might be one of the most important factors that make *S. fusiforme* well suited to withstand saline stress at the low intertidal zones.

References

Aguilera J., Bischof K., Karsten U. *et al.*: Seasonal variation in ecophysiological patterns in macroalgae from an Arctic fjord. II. Pigment accumulation and biochemical defence systems against high light stress. – Mar. Biol. **140**: 1087-1095, 2002.

Allakhverdiev S., Sakamoto A., Nishiyama Y. *et al.*: Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in *Synechococcus* sp. – Plant Physiol. **123**: 1047-1056, 2000.

Alric J.: Cyclic electron flow around photosystem I in unicellular green algae. – Photosynth. Res. **106**: 47-56, 2010.

Azzabi G., Pinnola A., Betterle N. *et al.*: Enhancement of non-photochemical quenching in the bryophyte *Physcomitrella patens* during acclimation to salt and osmotic stress. – Plant Cell Physiol. **53**: 1815-1825, 2012.

Beattie A., Hirst E., Percival E.: Studies on the metabolism of the Chrysophyceae. Comparative structural investigations on leucosin (chrysolaminarin) separated from diatoms and laminarin from the brown algae. – Biochem. J. **79**: 531-537, 1961.

Brányiková I., Maršálková B., Doucha J. *et al.*: Microalgae – novel highly efficient starch producers. – Biotechnol. Bioeng. **108**: 766-776, 2011.

Bräutigam K., Dietzel L., Kleine T. *et al.*: Dynamic plastid redox signals integrate gene expression and metabolism to induce distinct metabolic states in photosynthetic acclimation in *Arabidopsis*. – Plant Cell **21**: 2715-2732, 2009.

Bukhov N., Carpentier R.: Alternative photosystem I-driven electron transport routes: mechanisms and fuction. – Photosynth. Res. **82**: 17-33, 2004.

Chen H., Chen S., Jiang J.: Effect of Ca^{2+} channel block on glycerol metabolism in *Dunaliella salina* under hypoosmotic and hyperosmotic stresses. – PloS ONE **6**: e28613, 2011.

Dring M.: Stress resistance and disease resistance in seaweeds: the role of reactive oxygen metabolism. – Adv. Bot. Res. **43**: 175-207, 2005.

Gao S., Niu J., Chen W. *et al.*: The physiological links of the increased photosystem II activity in moderately desiccated *Porphyra haitanensis* (Bangiales, Rhodophyta) to the cyclic electron flow during desiccation and re-hydration. – Photosynth. Res. **116**: 45-54, 2013.

Gao S., Shen S., Wang G. *et al.*: PSI-driven cyclic electron flow allows intertidal macro-algae *Ulva* sp. (Chlorophyta) to survive in desiccated conditions. – Plant Cell Physiol. **52**: 885-893, 2011.

Gao S., Wang G.: The enhancement of cyclic electron flow around photosystem I improves the recovery of severely desiccated *Porphyra yezoensis* (Bangiales, Rhodophyta). – J. Exp. Bot. **63**: 4349-4358, 2012.

Gao S., Zheng Z., Gu W. *et al.*: Photosystem I shows a higher tolerance to sorbitol-induced osmotic stress than Photosystem II in the intertidal macro-algae *Ulva prolifera* (Chlorophyta). – Physiol. Plantarum **152**: 380-388, 2014.

Genty B., Briantais J., Baker N.: The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. – Biochim. Biophys. Acta **990**: 87-92, 1989.

Golding A., Johnson G.: Down-regulation of linear and activation of cyclic electron transport during drought. – Planta **218**: 107-114, 2003.

Harker M., Berkaloff C., Lemoine Y. *et al.*: Effects of high light and desiccation on the operation of the xanthophyll cycle in two marine brown algae. – Eur. J. Phycol. **34**: 35-42, 1999.

Huan L., Xie X., Zheng Z. *et al.*: Positive correlation between PSI response and oxidative pentose phosphate pathway activity during salt stress in an intertidal macroalga. – Plant Cell Physiol. **55**: 1395-1403, 2014

Huang W., Zhang S., Cao K.: Stimulation of cyclic electron flow during recovery after chilling-induced photoinhibition of PSII. – Plant Cell Physiol. **51**: 1992-1928, 2010.

Hwang E., Park C., Sohn C.: Culture condition on the early growth of *Hizikia fusiformis* (Phaeophyta). – Aquaculture **10**: 199-211, 1997.

Johnson M., Ruban A.: *Arabidopsis* plants lacking PsbS protein possess photoprotective energy dissipation. – Plant J. **61**: 283-289, 2010.

Johnson X., Alric J.: Interaction between starch breakdown, acetate assimilation, and photosynthetic cyclic electron flow in *Chlamydomonas reinhardtii*. – J. Biol. Chem. **287**: 26445-26452, 2012.

Klughammer C., Schreiber U.: An improved method, using saturating light pulses, for the determination of photosystem I quantum yield via P700+-absorbance changes at 830 nm. – Planta **192**: 261-268, 1994.

Klughammer C., Schreiber U.: Saturation pulse method for assessment of energy conversion in PSI. – PAM Application Notes **1**: 11-14, 2008.

Liu W., Ming Y., Li P. *et al.*: Inhibitory effects of hypo-osmotic stress on extracellular carbonic anhydrase and photosynthetic efficiency of green alga *Dunaliella salina* possibly through reactive oxygen species formation. – Plant Physiol. Bioch. **54**: 43-48, 2012.

Matsumura H., Miyachi S.: Cycling assay for nicotinamide adenine dinucleotides. – In: San Pietro A. (ed.): Methods in Enzymology. Pp. 465-470. Academic Press, New York 1983.

Maxwell K., Johnson G.: Chlorophyll fluorescence – a practical guide. – J. Exp. Bot. **51**: 659-668, 2000.

Murchie E., Niyogi K.: Manipulation of photoprotection to improve plant photosynthesis. – Plant Physiol. **155**: 86-92, 2011.

Niyogi K., Truong T.: Evolution of flexible non-photochemical quenching mechanisms that regulate light harvesting in oxygenic photosynthesis. – Curr. Opin. Plant Biol. **16**: 307-314, 2013.

Pang S., Chen L., Zhuang D. *et al.*: Cultivation of the brown alga *Hizikia fusiformis* (Harvey) Okamura: enhanced seedling production in tumbled culture. – Aquaculture **245**: 321-329, 2005.

Pang S., Shan T., Zhang Z. *et al.*: Cultivation of the intertidal brown alga *Hizikia fusiformis* (Harvey) Okamura: mass production of zygote-derived seedlings under commercial cultivation conditions, a case study experience. – Aquac. Res. **39**: 1408-1415, 2008.

Pang S., Zhang Z., Zhao H. *et al.*: Cultivation of the brown alga *Hizikia fusiformis* (Harvey) Okamura: stress resistance of artificially raised young seedlings revealed by chlorophyll fluorescence measurement. – J. Appl. Phycol. **19**: 557-565, 2007.

Parida A., Das A.: Salt tolerance and salinity effects on plants: a review. – Ecotox. Environ. Safe. **60**: 324-349, 2005.

Pfannschmidt T.: Chloroplast redox signals: how photosynthesis controls its own genes. – Trends Plant Sci. **8**: 33-41, 2003.

Sánchez F., Manzanares M., de Andres E. *et al.*: Turgor maintenance, osmotic adjustment and soluble sugar and proline

accumulation in 49 pea cultivars in response to water stress. – Field Crop. Res. **59**: 225-235, 1998.

Stiger V., Horiguchi T., Yoshida T. *et al*.: Phylogenetic relationships within the genus *Sargassum* (Fucales, Phaeophyceae), inferred from ITS-2 nrDNA, with an emphasis on the taxonomic subdivision of the genus. – Phycol. Res. **51**: 1-10, 2003.

Tokutsu R., Minagawa J.: Energy-dissipative supercomplex of photosystem II associated with LHCSR3 in *Chlamydomonas reinhardtii*. – P. Natl. Acad. Sci. USA **110**: 10016-10021, 2013.

Tseng C.: [*Flora algarum marinarum sinicarum*. Tomus III Phaeophyta, No II. Fucales.] Pp. 32-33. Science Press, Beijing 2000. [In Chinese]

Zou D.: Effects of elevated atmospheric CO_2 on growth, photosynthesis and nitrogen metabolism in the economic brown seaweed, *Hizikia fusiforme* (Sargassaceae, Phaeophyta). – Aquaculture **250**: 726-735, 2005.

Zou D., Gao K.: Photosynthetic characteristics of the economic brown seaweed *Hizikia fusiforme* (Sargassaceae, Phaeophyta), with special reference to its "leaf" and receptacle. – J. Appl. Phycol. **17**: 255-259, 2005.

Zou D., Gao K.: Photosynthetic acclimation to different light levels in the brown marine macroalga, *Hizikia fusiformis* (Sargassaceae, Phaeophyta). – J. Appl. Phycol. **22**: 395-404, 2010.

Zou D., Gao K., Ruan Z.: Seasonal pattern of reproduction of *Hizikia fusiformis* (Sargassaceae, Phaeophyta) from Nanao Island, Shantou, China. – J. Appl. Phycol. **18**: 195-201, 2006.

Zou D., Liu S., Du H. *et al*.: Growth and photosynthesis in seedlings of *Hizikia fusiformis* (Harvey) Okamura (Sargassaceae, Phaeophyta) cultured at two different temperatures. – J. Appl. Phycol. **24**: 1321-1327, 2012.