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Increase in unsaturated fatty acids in membrane lipids of *Suaeda salsa* L. enhances protection of photosystem II under high salinity

N. SUI[*], M. LI[**], K. LI[*], J. SONG[*], and B.-S. WANG[*,+]

Key Lab of Plant Stress Research, College of Life Science, Shandong Normal University, Jinan, 250014, P.R. China[*]
Shandong Academy of Agricultural Sciences, Jinan, 250100, P.R. China[**]

Abstract

In order to examine the possible role of unsaturated fatty acids in photosynthesis of halophytes under high salinity, the effect of salinity on plant growth, chlorophyll (Chl) content, photochemical efficiency of PSII, membrane lipid content and fatty acids composition of a C_3 euhalophyte *Suaeda salsa* L. was investigated. Salt stress induced a slight increase of the maximal photochemical efficiency of PSII (F_v/F_m), actual PSII efficiency (Φ_{PSII}), Chl *a* content and Chl *a*/*b* ratio. The unsaturated fatty acid content also increased under salt stress. The proportion of MGDG, DGDG, SQDG, and PC decreased, while the proportion of PG increased from 10.9% to 26.9% under salt stress. These results suggest that *S. salsa* displays high resistance to photoinhibition under salt stress and that increased concentration of unsaturated fatty acids in membrane lipids of *S. salsa* enhances the tolerance of photosystem II to salt stress.

Additional key words: chlorophyll; membrane lipid; photosystem; salt stress; *Suaeda salsa*; unsaturated fatty acids.

Introduction

Salinity is a major environmental factor that is known to reduce productivity of many plants. At present over 800 million hectares of land are salt-affected throughout the world (Munns and Tester 2008). Most of plant species are sensitive to salt stress.

In plants, cell membrane serves as a barrier that controls the passage of most ions and large molecules (Zhang *et al.* 2005). In plants and other organisms, the membrane structure and fluidity are affected by lipid composition and the degree of fatty acid desaturation (Mikami and Murata 2003). Membrane fluidity is known to affect bilayer permeability (Schuler *et al.* 1991), ATPase activity (Cooke and Burden 1990), and carrier-mediated transport (Deuticke and Haest 1987). Lipid membrane fluidity is defined by variable unsaturated fatty acid level. Many reports indicate that changes in unsaturated fatty acids content can improve plant tolerance to environmental stresses such as cold, heat and drought (Dakhma *et al.* 1995, Olsson 1995, Matos *et al.* 2002, Sui *et al.* 2007a,b; Liu *et al.* 2008). In higher plants, the most abundant membrane lipids are glycolipids, including monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG), sulfoquinovosyldiacylglycerol (SQDG) and phosphatidylglycerol (PG), which is the only phospholipid present in photosynthetic membranes. The role of glycerolipids in the membrane functions has been exhaustively studied (Siegenthaler 1998).

The lipid composition of living cell membrane generally adapts to prevailing environmental and physiological conditions. Several reports have suggested that lipids are involved in the protection of photosystem against salt stress. During adaptation of barley (*Hordeum vulgare* L.) seedlings to extremely high concentrations of

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[+]Corresponding author; tel.: +86 531 86180197, e-mail: bswang@sdnu.edu.cn
Abbreviations: 16:0 – palmitic acid; 16:1(3t) – Δ3-*trans*-hexadecenoic; 18:0 – stearic acid; 18:1 – oleic acid; 18:2 – linoleic acid; 18:3 – linolenic acid; Chl – chlorophyll; DGDG – digalactosyldiacylglycerols; F_o – initial fluorescence of the dark-adapted state; F_v – variable fluorescence; F_m – maximal fluorescence of the dark-adapted state; F_s – the steady-state fluorescence; F_m' – maximal fluorescence in the light-adapted state; F_v/F_m – maximal photochemical efficiency of PSII; DBI – double bond index; MGDG – monogalactosyldiacylglycerols; PC – phosphatidylcholines; PG – phosphatidylglycerols; Φ_{PSII} – the quantum yield of PSII electron transport; SQDG – sulphoquinovosyldiacylglycerols.
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NaCl in the root space, the content of galactolipids in chloroplast membranes decreased considerably (Muller and Santarius 1978). Using wild-type and *desA*1 cells of *Synechococcus*, unsaturation of fatty acids in membrane lipids protected photosystem II (PSII) and photosystem I (PSI) against both rapid and slow phase of NaCl-induced inactivation. The unsaturation of fatty acids was radically effective in protecting the photosynthetic machinery during the slow phase (Allakhverdiev *et al.* 2001).

The Chenopodiaceae *Suaeda salsa* L., a C_3 euhalophytic herb, is native of saline soils, or even grows in the intertidal zone of the Yellow River Delta in the north of China, where soil salt content is often higher than 3% (Wang *et al.* 2001).

Previous studies on unsaturated fatty acids in response to salt stress were carried out on bacterium and the nonhalophyte plants. Some studies also investigated SQDG content and the ratio of 18:2/18:3 in SQDG during salt stress in the halophyte (Ramani *et al*. 2004, Ben Hamed *et al*. 2005). Our recent studies have shown that high salinity (100–400 mM NaCl) leads to a slight increase of CO_2 assimilation rate (Lu *et al.* 2002, 2003). In these experiments, *S. salsa* has shown high resistance not only to salinity stress but also to photoinhibition even when treated with high salinity as high as 400 mM NaCl and exposed to full sunlight (Lu *et al.* 2002). These results suggest that *S. salsa* has some effective mechanisms to protect photosystem under salt stress.

The objective of the present study was to investigate whether the unsaturation of fatty acids in membrane lipids has effects on protection of PSII under high salinity in the euhalophyte of *S. salsa*.

Materials and methods

Plant material and NaCl treatment: Seeds of *S. salsa* L. were collected from Yellow River Delta, Shandong Province, P. R. China. After being sterilized in 0.5% $HgCl_2$ for 3 min, the seeds were washed and germinated in plastic plates filled with sand then kept in the dark at 25°C for 3 days, watering with 1/2 MS solution. After germination the seedlings were transferred to greenhouse and cultivated under a 12 h d^{-1} photoperiod, 600 μmol m^{-2} s^{-1} light intensity, 28°C /23°C day/night temperature and 70–80% relative humidity. Seedlings with 2–3 branches were subjected to 300 mM NaCl treatment. 1 mM NaCl treatment was used as control. NaCl concentration was stepped up in 50 mM every 12 h until final concentration of 300 mM. Physiological parameters were checked after 5-d treatment.

Pigment analysis: For leaf Chl content analyses, leaves from five plants per plot were extracted by 80% acetone for 48 h. Chl *a* and *b* contents were measured using spectrophotometer according to Zhao *et al.* (2002).

Lipid extraction and analysis: *S. salsa* leaf tissue was harvested and frozen immediately in liquid nitrogen. Lipids were extracted as described by Siegenthaler and Eichenberger (1984) and separated by two-dimensional thin layer chromatography (TLC) (Xu and Siegenthaler 1997). For quantitative analysis, lipids were separated by TLC, scraped from the plates, and used to prepare fatty acid methyl esters. The fatty acid composition of individual lipids was determined using gas chromatography (*GC-9A, Shimadzu*, Japan) as described by Chen *et al.* 1994.

Chl fluorescence was measured using a portable fluorometer (*FMS2, Hansatech*, King's Lynn, UK) following to the protocol described by van Kooten and Snel (1990). Minimal fluorescence (F_o) with all PSII reaction centers open was determined by modulated light which was low enough not to induce any significant variable fluorescence (F_v). Maximal fluorescence (F_m) with all reaction centers closed was determined by 0.8-s saturating light of 8,000 μmol m^{-2} s^{-1} on a dark-adapted leaf (adapted 15 min in darkness). Then the leaf was illuminated by an actinic light of 500 μmol m^{-2} s^{-1}. Steady-state fluorescence (F_s) was recorded when the leaf reached steady-state photosynthesis. A second 0.8-s saturating light of 8,000 μmol m^{-2} s^{-1} was given to determine maximal fluorescence in the light-adapted state (F_m'). Maximal photochemical efficiency (F_v/F_m) of PSII was expressed as: $F_v/F_m = (F_m–F_o)/F_m$. Quantum yield of PSII electron transport was: $\Phi_{PSII} = (F_m'–F_s)/F_m'$.

Leaf fresh mass and dry mass per plant: The field plant material was first cleaned with distilled water. After absorbing water using tissue paper, fresh mass (FM) of plant material was measured. Dry mass (DM) was measured after drying plants at 80°C. Water content (WC) was then determined: WC = (FM–DM)/FM × 100%.

Statistical analysis: Data were transformed (arcsine) before statistical analysis in order to ensure homogeneity of variance. Multiple comparisons were performed between different environmental conditions using *Duncan*'s test at the 0.05 significance level. All tests were performed with *SPSS Version 16.0 for Windows* (*SPSS*, Chicago. IL, USA).

Results

***S. salsa* growth and water content**: The data showed the growth changes under salt treatment. The growth of *S. salsa* was significantly increased by 300 mM NaCl treatment compared to that of 1 mM NaCl (Fig. 1). Applying 300 mM NaCl increased both fresh and dry mass. The fresh and dry mass at 1 mM NaCl treatment were 2.59 g, and 0.27 g per plant, respectively. Under 300 mM NaCl treatment the fresh mass was 4.65 g but the dry mass was only 0.43 g per plant. The water content was 89.6% at 1 mM NaCl treatment and 90.8% at 300 mM NaCl treatment, which was not significantly different.

PSII photochemical efficiency: To check whether NaCl treatment alter the light system of photosynthesis, we measured maximal photochemistry of PSII and quantum yield of PSII electron transport. As shown in Fig. 2, NaCl treatment had very little effect on the F_v/F_m ratio, and thereby on maximal photochemistry of PSII. This suggested that PSII are rather tolerant to NaCl and that NaCl stress had no effect on PSII photochemistry in dark-adapted leaves. In order to check for modifications in light-adapted leaves, PSII photochemistry was also determined in light-adapted leaves, *i.e.* leaves under steady-state photosynthesis. Φ_{PSII} increased by 20.2% under 300 mM NaCl treatment, which indicated that photosynthetic electron transport was increased under NaCl stress.

Chl *a* and *b* content and Chl *a*/*b* ratio: Applying 300 mM NaCl treatment increased the content of Chl *a* by 8.1% and decreased the content of Chl *b* by 2.7%. The ratio of Chl *a*/*b* was increased from 2.86 at 1 mM NaCl treatment to 3.18 at 300 mM NaCl treatment.

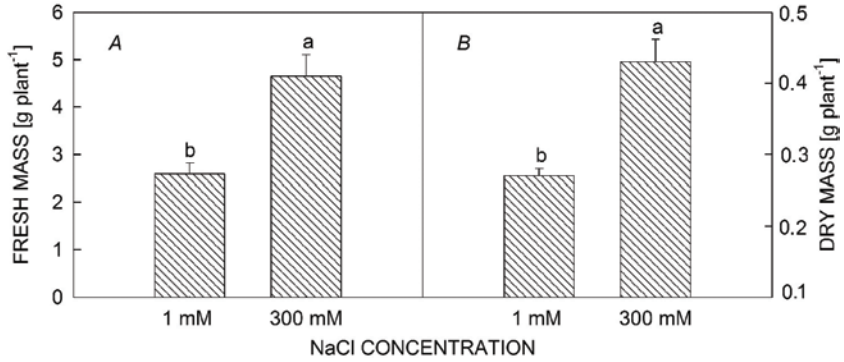

Fig. 1. Changes of leaf fresh mass and dry mass of *S. salsa* at NaCl stress. Each point represents the means ± SD of five measurements on each of five plants. Means identified by *different letters* are significantly different at $P<0.05$.

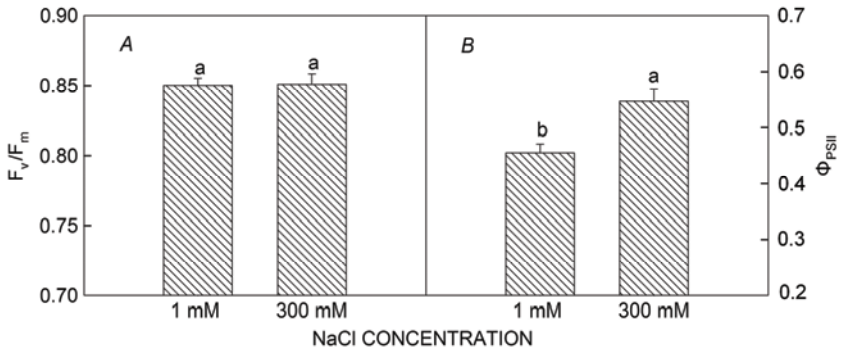

Fig. 2. Effect of NaCl stress on F_v/F_m (*A*) and Φ_{PSII} (*B*) in *S. salsa*. *Vertical bars* represent standard deviations, $n = 5$. Means identified by *different letters* are significantly different at $P<0.05$.

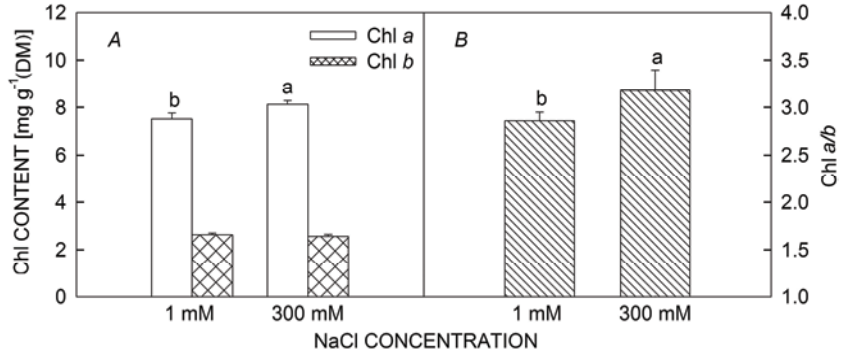

Fig. 3. Changes of chlorophyll (Chl) content (*A*) and Chl *a*/*b* (*B*) of *S. salsa* at NaCl stress. Chl *a* and *b* have absorption maxima at 663 nm and 645 nm, respectively. Each point represents the means ± SD of five measurements on each of five plants. Means identified by *different letters* are significantly different at $P<0.05$.

Table 1. Fatty acid composition of membrane lipids in *S. salsa* leaves. Data are expressed as mean values ± SD (n = 3) and are presented as mole percentage. Means identified by *different letters* are significantly different at $P<0.05$. MGDG – monogalactosyldiacylglycerols; DGDG – digalactosyldiacylglycerols; SQDG – sulphoquinovosyldiacylglycerols; PG – phosphatidylglycerols; PC – phosphatidylcholines; DBI – double bond index.

Fatty acid	MGDG		DGDG		SQDG		PG		PC	
[mol %]	1 mM	300 mM	1 mM	300 mM	1 mM	300 mM	1 mM	300 mM	1 mM	300 mM
16:0	11.0 ± 0.4^a	-	20.6 ± 2.0^a	19.1 ± 1.7^a	31.1 ± 3.2^a	29.2 ± 1.9^a	27.4 ± 1.7^a	25.6 ± 2.7^a	43.3 ± 4.7^a	43.8 ± 3.2^a
16:1(3t)	-	-	-	-	-	-	9.4 ± 0.2^b	14.1 ± 0.1^a	-	-
18:0	13.8 ± 1.0^a	14.1 ± 0.9^a	19.0 ± 1.2^a	7.8 ± 0.3^b	21.8 ± 2.3^a	7.9 ± 0.5^b	19.9 ± 0.6^a	10.1 ± 0.6^b	32.1 ± 2.1^a	29.0 ± 3.1^a
18:1	1.5 ± 0.0^b	3.8 ± 0.1^a	-	1.6 ± 0.0^a	5.6 ± 0.7^b	8.7 ± 0.1^a	-	2.3 ± 0.0^a	-	-
18:2	4.4 ± 0.1^a	-	1.8 ± 0.0^b	6.6 ± 0.1^a	30.2 ± 2.8^a	35.0 ± 2.1^a	28.9 ± 1.6^a	27.9 ± 1.4^a	-	-
18:3	69.2 ± 4.1^b	82.1 ± 5.6^a	58.6 ± 3.7^a	64.9 ± 5.9^a	11.3 ± 0.7^b	19.2 ± 1.8^a	14.4 ± 1.0^b	20.0 ± 0.5^a	24.5 ± 1.9^a	27.3 ± 1.9^a
DBI	218.0	250.1	179.4	199.7	73.6	81.8	101.0	118.1	99.9	136.3

Table 2. Composition of lipid classes in *S. salsa* leaves at different salinities. Each value is the mean ± SD of three determinations. Means identified by *different letters* are significantly different at $P<0.05$. MGDG – monogalactosyldiacylglycerols; DGDG – digalactosyldiacylglycerols; SQDG – sulphoquinovosyldiacylglycerols; PG – phosphatidylglycerols; PC – phosphatidylcholines.

Lipid class	Lipid content [mol %]	
	1 mM NaCl	300 mM NaCl
MGDG	25.6 ± 2.2[a]	23.2 ± 1.5[a]
DGDG	28.7 ± 2.3[a]	27.1 ± 2.0[a]
SQDG	23.1 ± 1.3[a]	15.7 ± 0.7[b]
PG	10.9 ± 0.3[b]	26.9 ± 1.3[a]
PC	11.7 ± 0.5[a]	7.1 ± 0.1[b]

Lipid content and fatty acids composition: We analyzed the effects of salinity on fatty acid composition of membrane lipids. After 300 mM NaCl treatment, the unsaturated fatty acid content and the DBI (DBI =18:1 × 1 + 18:2 × 2 + 18:3 × 3) of the major membrane lipid of MGDG, DGDG, SQDG, PG, and PC (Table 1) were significantly increased. Unsaturated fatty acid contents, oleic acid (18:1) and linolenic acid (18:3) of MGDG, 18:1, linoleic acid (18:2) and 18:3 of DGDG, 18:1, 18:2 and 18:3 of SQDG, 18:1 and 18:3 of PG and 18:3 of PC increased. The MGDG contained predominantly 18:3 with smaller proportions of palmitic acid (16:0). PG contained a considerable amount of Δ3-*trans*-hexadecenoic (16:1). And the 16:1 content was also increased by salt stress.

Table 3. Constituent fatty acids of total lipids in *S. salsa* leaves at different salinities. Each value is the mean ± SD of three determinations. Means identified by different letters are significantly different at $P<0.05$.

Fatty acid	Fatty acid composition [mol %]	
	1 mM NaCl	300 mM NaCl
16:0	29.5 ± 1.9[a]	28.1 ± 1.1[a]
16:1(3t)	1.4 ± 0.8[b]	3.0 ± 0.0[a]
18:0	20.1 ± 0.9[a]	11.9 ± 0.3[b]
18:1	2.3 ± 0.0[b]	3.2 ± 0.0[a]
18:2	15.7 ± 0.3[b]	19.9 ± 0.6[a]
18:3	31.0 ± 2.1[a]	33.9 ± 1.8[a]
DBI	126.7	144.7

Under both 1 and 300 mM NaCl treatment, the levels of MGDG, DGDG, SQDG, and PC decreased by 9.4%, 5.6%, 32.0%, and 39.3%, respectively. Only PG level increased from 10.9% to 26.9%.

In various treatments, the fatty acids content of the total lipid fraction varied according to the NaCl concentration (Table 3). We observed an increase in the proportion of unsaturated fatty acids and a decrease in the proportion of saturated fatty acids under salt stress. Under 300 mM NaCl treatment, 16:0 and 18:0 decreased 4.7% and 40.8%, 16:1, 18:1, 18:2, and 18:3 increased 114.3%, 39.1%, 26.8%, and 9.4%, respectively, as found for 1 mM NaCl treatment. These data reflect that the content of unsaturated fatty acids increases under salt stress in *S. salsa* leaves, while the content of saturated fatty acids decreases.

Discussion

In the present study, we have observed that the growth of the *S. salsa* plant is significantly increased by salt treatment. Salinity has no significant effects on leaf water content. This may be mainly attributed to the accumulation of Na^+ and Cl^-, which can markedly induce leaf succulence of the species (Qiu *et al.* 2001). The increase in sodium and chloride content without changes in water content may induce succulence of the *S. salsa* shoots.

PSII is believed to play a key role in leaf photosynthesis in responses to environmental perturbations (Baker 1991). Several environmental stresses, particularly heat and high light stress, have been shown to have their primary target in the PSII complex (Berry and Björkman 1980, Aro *et al.* 1993). The euhalophyte *S. salsa* showed high resistance not only to salinity stress but also to photoinhibition at high salinity (Lu *et al.* 2002). This concept is strongly supported by our results. The PSII activity was not affected by salt stress, however, treatment of NaCl as high as 300 mM increased Φ_{PSII} by only about 20%, suggesting that PSII is rather tolerant to salt stress and that *S. salsa* has effective mechanisms to protect photosystem under salt stress.

Chl is the most important component of light harvesting complex (LHCII), which acts as an antenna to absorb light energy. Chl *a* molecules are critical components in light-harvesting and electron transfer reaction in photosynthesis. They can regulate light absorption, transition, and distribution. Treatment of NaCl as high as 300 mM increased Chl *a* content and Chl *a*/*b* ratio (Fig. 3). Higher Chl content inevitably results in higher photochemical efficiency of PSII, and then higher production (Figs. 1,2,3). Chl *a*/*b* reflects the stacking extent of thylakoid membrane, *i.e.* the proportion of stacked thylakoid membrane (Staehelin 2003). An increase in Chl *a*/*b* is generally interpreted as an indication of less stacking (Anderson 1986). Large changes in stacking would hypothetically require LHC synthesis and/or degradation in response to long-term environmental change (Carter and Cheeseman 1993). The increase of Chl *a* content means higher light absorption, higher transition and higher distribution, which might result in photodamage of the photosystem under salt stress. With higher Chl *a*/*b* ratio, thylakoid stacking extent is less and the content of LHCII is lower. Light energy harvested by LHCII can be used adequately and photoinhibition is more difficult to occur (Fig. 2).

The hydrophobic lipid interior of the membrane acts as a barrier to the passage of many ions and large molecules (Upchurch 2008). Moreover, membrane integrity and the functionality of integral membrane proteins are maintained by membrane structure and fluidity. In a previous study, we showed that the unsaturated fatty acids in membranes lipids protects the photosynthesis system against chilling stress under low irradiance by alleviating photoinhibition of PSII and PSI (Sui *et al.* 2007a). The present results show that high salt levels increases the unsaturated fatty acids content of membrane lipids (Tables 1, 3), and an increase of phosphatidylglycerol (PG) is shown (Table 2). PG is an integral component of photosynthetic membranes. It is important for both development and functioning of the photosynthesis apparatus (Domonkos *et al.* 2008). In higher plants, PG contributes to the development of chloroplasts (Hagio *et al.* 2002). Thus, the increase of PG concentration in the euhalophyte *S. salsa* may be important for PSII tolerance to salt stress.

The content of galactolipids of MGDG, DGDG, and SQDG decreased considerably. It is suggested that the decrease in content of galactolipids is one of the factors causing increased salt resistance to extreme salinity. A change in the ratio of a bilayer forming lipid (DGDG) to an inverse hexagonal forming lipid (MGDG) (DGDG/MGDG ratio) can affect the structure and microviscosity of membranes and the accumulation of phospholipids in leaves and it can perturb resistance of organisms to environmental stresses (*e.g*. salt stress). Study has proved that the increase of the DGDG/MGDG ratio and fatty acid unsaturation can increase tolerance of plants to stress (Gigon *et al.* 2004). The ratio of DGDG/MGDG at 300 mM NaCl treatment was 1.17, which was higher than 1.12 at 1 mM NaCl treatment, suggesting higher tolerance to salt stress.

Overexpression of x-3 desaturases in transgenic tobacco plants was shown to increase tolerance to salt and drought stresses (Zhang *et al.* 2005), suggesting that plant tolerance to salt and drought is dependent on unsaturated fatty acid levels. (Berberich *et al.* 1998, Mikami and Murata 2003). *Synechocystis* mutants, lacking x-6 and x-3 desaturase activities had reduced tolerance to salt stress (Allakhverdiev *et al.* 1999). Introduction of two sunflower x-6 desaturases genes into yeast increased their tolerance to NaCl and freezing (Rodrıguez-Vargas *et al.* 2007). We show that the unsaturated fatty acids in lipid membrane protect PSII from NaCl stress, which is consistent with the result in *Synechococcus* that the combination of light and the fatty acid unsaturation is shown to be the most effective way to protect the photosynthetic machinery (Allakhverdiev *et al.* 2001). A possible explanation may be that ion (Na^+ or K^+) channels and the Na^+/H^+ antiport systems locate on the plasma membrane and their activities are dependent on the degree of unsaturated fatty acids in lipid membrane. The increase of unsaturated fatty acids in lipid membrane may increase membrane fluidity resulting in activation of Na^+/H^+ antiporter(s) and/or H^+-ATPase(s) and thereby protects photosystem activities (Allakhverdiev *et al.* 2001). The increase of unsaturated fatty acids also may stimulate the synthesis of Na^+/H^+ antiporter(s) and/or H^+-ATPase(s). The increased density of the antiport system in the membrane mediates perhaps decreasing cytosolic concentration of Na^+ ions to allow the protection of the plant photosystem against salt aggravation (Inaba *et al.* 2001).

In conclusion, we demonstrated that the content of unsaturated fatty acids in euhalophyte *S. salsa* increased by salt stress. The increase of unsaturated fatty acids in membrane lipids can increase the photosystem tolerance to salt stress. But, which enzyme is most effective in increase of the unsaturation of fatty acids in euhalophyte of *S. salsa*, and the regulation mechanism of unsaturated fatty acids in the tolerance of PSII to salt stress in the species remains to be further studied.

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