



Positive effects of NaCl on the photoreaction and carbon assimilation efficiency in *Suaeda salsa*

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ABSTRACT

Suaeda salsa L. is a typical euhalophyte and can be used as a model halophyte for research on salt tolerance. *S. salsa* seedlings were cultured with 0, 200 and 500 mM NaCl for 2 and 14 days. The results revealed that 200 mM NaCl promoted the shoot dry weight, net photosynthetic rate (Pn), chlorophyll content, electron transfer rate, NADPH level, activities of ferredoxin-NADP oxidoreductase, ribulose-1, 5-bisphosphate carboxylase (Rubisco) and Rubisco activase, particularly the Rubisco activity, chlorophyll content and Pn, when the seedlings were treated with 200 mM NaCl for 14 days. Moreover, 500 mM NaCl had no adverse effects on those parameters. In conclusion, NaCl improved the photoreaction and carbon assimilation efficiency of *S. salsa*. The increased Rubisco activity and chlorophyll content may play critical roles in the enhancement of the photosynthetic efficiency in *S. salsa* under saline conditions, which may explain why *S. salsa* can produce the highest biomass at approximately 200 mM NaCl.

1. Introduction

Environmental stresses, such as drought and salinity, have always been the biggest factors that deleteriously affect agricultural production (Bohnert et al., 1995), and salt stress is one of the most important abiotic stresses (Rasool et al., 2013). More than 800 million hectares of land around the world are affected by soil salinization (Munns, 2005). Soil salinity leads to reduced crop yields, and urban expansion reduces the area of cultivated land (Shabala, 2013), which both seriously affect global food security. Therefore, developing agriculture that tolerates saline conditions is one of the ways to increase the area of cultivated land and increase the production of food (Edrisi et al., 2020).

Photosynthesis is the most basic and critical physiological process in plants (Xu et al., 2015), and it is one of the main processes of plant physiological metabolism that is affected by salinity (Chaves et al., 2009). Salt stress can cause osmotic stress, ion toxicity and produce reactive oxygen species (ROS) that damage the cell membrane and enzymatic systems (Zhu, 2001), subsequently causing damage to the chloroplast photosynthetic system. Salt stress causes the stomata to close and restricts the transport of mesophyll cell CO₂. The chlorophyll

content, Pn, and electron transport rate (ETR) are reduced, and the enzyme activity of Calvin cycle is impaired, which results in a decrease in the plant biomass of crops, such as rice (*Oryza sativa*) (Moradi and Ismail, 2007), wheat (*Triticum aestivum*) (Ouerghi et al., 2000), and maize (*Zea mays*) (Hichem et al., 2009). However, previous studies have found that the photosynthesis, growth, and reproduction of some halophytic species are not significantly inhibited or are even promoted under saline conditions (Li et al., 2012; Guo et al., 2015, 2018; Wungrampha et al., 2018). Rubisco (Parry et al., 2003) and Rubisco activase (RCA) (Hazra et al., 2015) are key enzymes for carbon fixation and reduction, and changes in the activity of these catalysts are critical to the efficiency of the Calvin cycle. However, changes in these catalysts under salinity have rarely been studied (He et al., 2014), which may help to understand why salinity can improve photosynthesis and plant growth in halophytes. Therefore, studying the mechanism of salt tolerance in halophytes, particularly during photosynthesis, can provide a theoretical basis for crop improvement and breeding (Flowers, 2004).

Halophytes can survive to reproduce in environments where the concentration of salt is approximately 200 mM NaCl or higher (Flowers and Colmer, 2008), and they are regarded to be valuable for

Abbreviations: Electron transport rate, ETR; Ferredoxin-NADP oxidoreductase, FNR; Ribulose-1 5-bisphosphate carboxylase, Rubisco; Rubisco activase, RCA.

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understanding plant salt tolerance and developing saline agriculture (Song and Wang, 2015; Custódio et al., 2021; Mujeeb et al., 2021; You et al., 2021). *Suaeda salsa* L. is a typical euhalophyte that is highly tolerant to salt (Wang et al., 2015; Chen et al., 2016; Li et al., 2016; Liu et al., 2021a) and can be used as a model system for research on plant salt tolerance (Song and Wang, 2015). *S. salsa* can also be used as a vegetable and oil crop and has substantial medicinal value (Song and Wang, 2015; Zhao et al., 2018, 2019). The photosynthetic capacity and biomass of *S. salsa* improve significantly at 200 mM NaCl (Zhang et al., 2005; Song et al., 2009a), but the mechanism is not yet clear. High salinity had no adverse effect on the actual PSII efficiency (Φ_{PSII}) in either a dark-adapted or light-adapted state (Lu et al., 2003). However, the response of halophytes, such as *S. salsa*, to salinity during carbon assimilation has rarely been studied. Therefore, in this study, the effect of salinity on ETR, ferredoxin-NADP oxidoreductase (FNR) activity and NADPH level in chloroplasts during the photoreaction stage, as well as the activities of Rubisco and RCA, during the carbon assimilation stage were investigated. This study aimed to understand how salinity promotes the photosynthesis and growth of *S. salsa* at saline level of 200 mM NaCl.

2. Materials and methods

2.1. Seed collection

Seeds of *S. salsa* were collected from saline soils (N37°20' E118°36') in the Yellow River Delta in Shandong Province, China. The seeds were dried naturally and stored at <4 °C for four months before use.

2.2. Plant culture and experimental design

Brown seeds were sown in plastic pots (with drainage holes) filled with washed river sand. The seedlings were cultured in a greenhouse under natural light. The temperature was 24 ± 4 °C during the day and 18 ± 4 °C at night. The seedlings were watered with 1 mM NO_3^- -N nutrient solution (Liu et al., 2018). The pH of the solution was adjusted to 6.2 ± 0.1 with KOH and H_2SO_4 (Li and Song, 2019).

After the seedlings had been pre-cultured for 50 days, 15 seedlings remained in each pot, and they were treated with 0, 200, and 500 mM NaCl; the NaCl was prepared with a nutrient solution of 1 mM NO_3^- -N (Li and Song, 2019). The NaCl was added in increments of 50 mM per day to avoid osmotic shock (Liu et al., 2021b). After levels of 200 and 500 mM of NaCl were simultaneously reached for 2 and 14 days, mature fresh leaves in the same position were used for the experiments.

2.3. Measurement of biomass

The shoots of plants in each pot were sampled after 14 days of treatment with 200 and 500 mM NaCl. There were three pots for each treatment. The leaves were dried at 80 °C for 3 days, and their dry weight (DW) was measured. There were three replicates for each concentration of NaCl.

2.4. Determination of chlorophyll content and net photosynthetic rate

Fresh mature leaves (0.3 g for each replicate) in the same leaf position were ground in 80% acetone, and the chlorophyll content was determined by spectrophotometry (UV-120-02 Spectrophotometer; Shimadzu, Kyoto, Japan) (Ma et al., 2020). There were three replicates for each concentration of NaCl.

Mature leaves in the same leaf position were selected to measure the Pn. A portable photosynthesis measurement system (LI 6400; LI-COR, Inc., Lincoln, NE, USA) was used to measure the net photosynthetic rate (Duan et al., 2018). Six replicates were established for each concentration of NaCl.

2.5. Measurement of the maximal efficiency of PSII photochemistry and electron transfer rate

A portable pulse-modulated fluorometer (FMS-2; Hansatech, King's Lynn, UK) was used to determine the maximal efficiency of PSII photochemistry (F_v/F_m) and the ETR in the leaves. The steady-state fluorescence (F_s) and maximum fluorescence (F_m') under light were measured. The leaves were subsequently adapted to darkness for 30 min, and the minimum fluorescence (F_0) and maximum fluorescence (F_m) were measured (Song et al., 2009b). Three replicates were established for each concentration of NaCl.

2.6. Determination of the activities of ferredoxin-NADP oxidoreductase, ribulose-1, 5-bisphosphate carboxylase and rubisco activase

A total of 0.3 g of mature leaves were placed in a pre-cooled mortar, and the leaves were ground on ice with chilled 50 mM Tris buffer at pH 7.4. The supernatant was extracted by centrifugation and stored at -20 °C. The activity of FNR was assayed using a plant ELISA kit (Shanghai Huding Biotechnology Co., Ltd., Shanghai, China). A microplate reader (Spectra Max M5; Molecular Devices, San Jose, CA, USA) was used to assay the activity of the enzyme according to the manufacturer's instructions (Zhao et al., 2018). Three replicates were established for each concentration of NaCl.

The activities of Rubisco and RCA were assayed as described for FNR.

2.7. Determination of the level of NADPH

A total of 2 g of mature leaves were homogenized by grinding in a pre-cooled mortar on ice with pre-cooled Tris buffer for homogenization. The leaf chloroplasts were extracted by differential centrifugation, and the extract was diluted to an A_{660} of 1.0. The homogenate was incubated in an ice bath for later use. The level of NADPH was determined as described in Section 2.6. There were three replicates for each concentration of NaCl.

2.8. Statistical analysis

The data within 2 and 14 days were subjected to a one-way analysis of variance (ANOVA) using SASTM software (SAS Institute, Inc., 1989). The values provided are the measured averages of three replicate plants, and the comparison of the averages was determined by a least significant difference (LSD) test. The difference was considered significant at $P < 0.05$.

3. Results

3.1. Effect of salinity on shoot dry weight, Pn and chlorophyll content

The shoot dry weight at 200 mM NaCl was higher than that at 0 mM NaCl (control) after treatment with salinity for 14 days, while 500 mM NaCl did not decrease the value compared with the control (Figs. 1a and S1). The changes in the Pn in the leaves (Fig. 1b) were consistent with the shoot dry weight. For example, the shoot dry weight was 1.22- and 1.11-fold higher than that at 200 and 500 mM NaCl than at 0 mM NaCl, respectively, and the Pn was 1.28- and 0.98-fold those at 0 mM NaCl, respectively (Fig. 1).

The contents of chlorophyll *a*, chlorophyll *b*, and chlorophyll *a*+*b* at 200 mM NaCl were significantly higher than those at 0 and 500 mM NaCl when the seedlings were treated with salinity for 14 days (Fig. 2). For example, the content of chlorophyll *a*+*b* at 200 and 500 mM NaCl was 1.25- and 1.08-fold higher than that at 0 mM NaCl, respectively (Fig. 2).

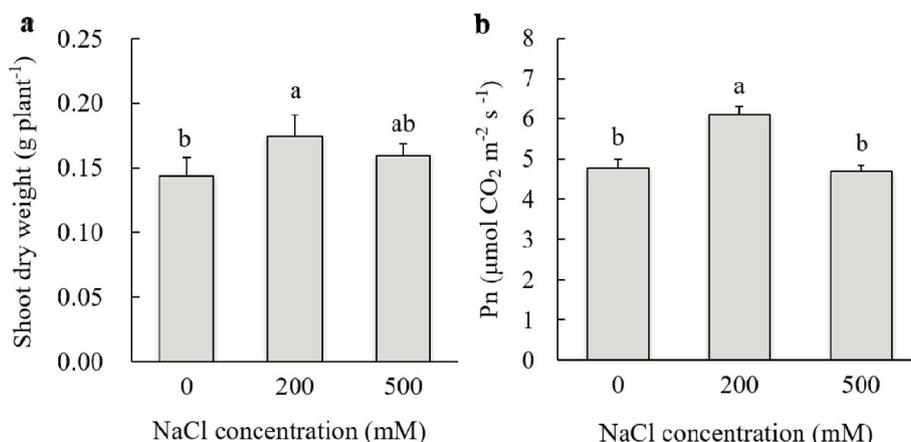


Fig. 1. Effect of salinity on the shoot dry weight (a) and net photosynthetic rate (Pn) (b) of *Suaeda salsa*. Seedlings were treated with 0, 200, and 500 mM NaCl for 14 days. For each group of 3 bars, the means with different letters are significantly different at $P < 0.05$. Vertical bars indicate the standard errors of means ($n = 3$ for shoot dry weight and $n = 6$ for Pn).

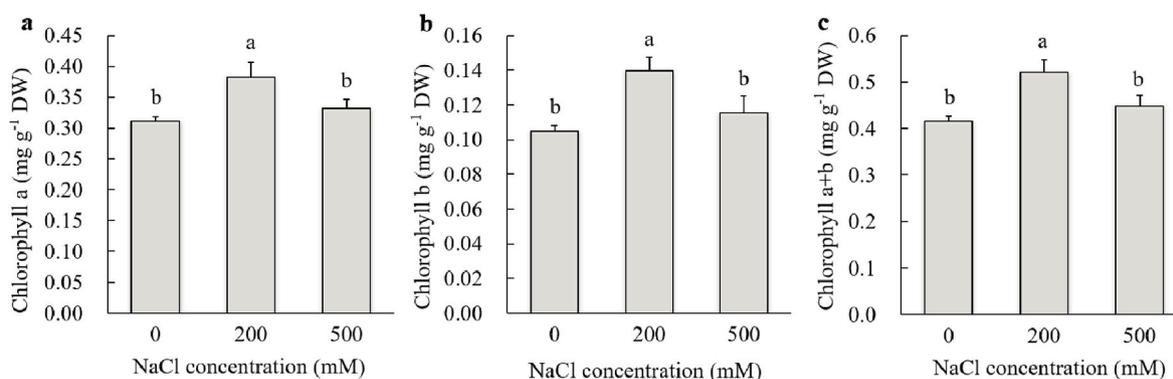


Fig. 2. Effect of salinity on the contents of chlorophyll a (a), chlorophyll b (b), and chlorophyll a+b (c) in *Suaeda salsa*. The seedlings were treated with 0, 200, and 500 mM NaCl for 14 days. For each group of 3 bars, the means with different letters are significantly different at $P < 0.05$. Vertical bars indicate the standard errors of means ($n = 3$).

3.2. Effect of salinity on Fv/Fm and ETR

The F_v/F_m did not change under different concentrations of NaCl during the entire duration of the experiment (Fig. 3a). Salinity had no significant effect on the ETR when seedlings were treated with salinity for 2 days. When the seedlings were treated with salinity for 14 days, the ETR gradually increased with the increase in the concentration of NaCl (Fig. 3b). The ETR at 200 and 500 mM NaCl is 1.07- and 1.13-fold higher than that at 0 mM NaCl, respectively (Fig. 3b).

3.3. Effects of salinity on the FNR activity and NADPH level

The activity of FNR decreased with the increase in concentration of NaCl when the seedlings were treated with different concentrations of NaCl for 2 days. However, the value gradually increased with the increase in NaCl when the seedlings were treated with salinity for 14 days (Fig. 4a). Simultaneously, the level of NADPH increased with the increase in concentration of NaCl during the entire time course, particularly at 500 mM NaCl (Fig. 4b). The level of NADPH at 200 and 500 mM

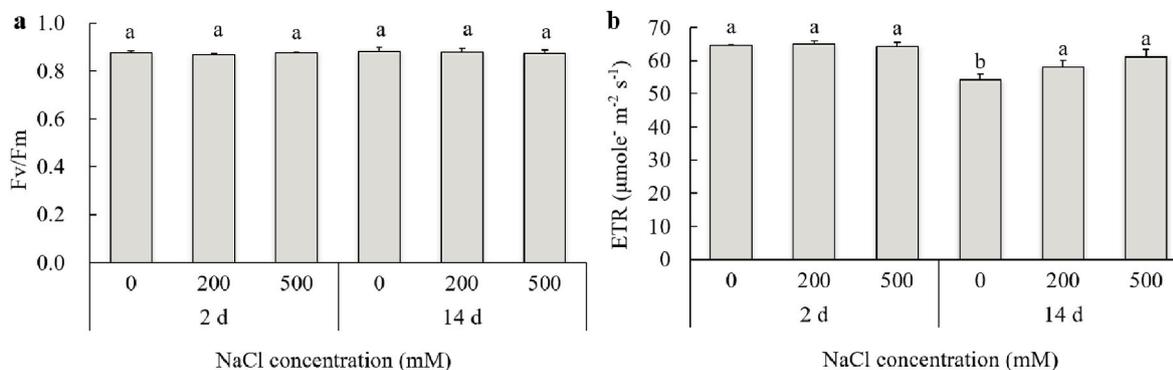


Fig. 3. Effect of salinity on the maximal efficiency of PSII photochemistry (F_v/F_m) (a) and the electron transfer rate (ETR) (b) in *Suaeda salsa*. The seedlings were treated with 0, 200, and 500 mM NaCl for 2 and 14 days. For each group of 3 bars at 2 or 14 days, the means with different letters are significantly different at $P < 0.05$. Vertical bars indicate the standard errors of means ($n = 3$).

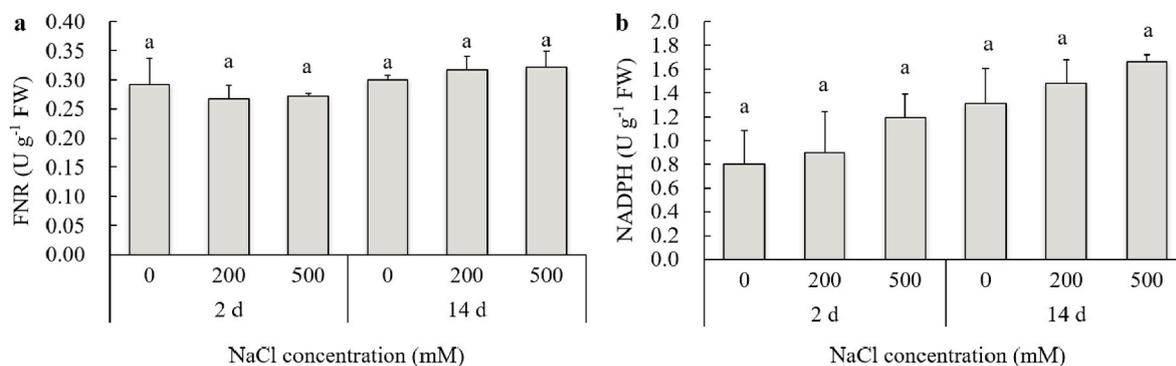


Fig. 4. Effect of salinity on the FNR activity (a) and NADPH activity (b) of *Suaeda salsa*. The seedlings were treated with 0, 200, and 500 mM NaCl for 2 and 14 days. For each group of 3 bars at 2 or 14 days, the means with different letters are significantly different at $P < 0.05$. Vertical bars indicate the standard errors of means ($n = 3$).

NaCl was 1.13- and 1.27-fold higher than those at 0 mM NaCl, respectively, when the seedlings were treated with salinity for 14 days (Fig. 4b).

3.4. Effects of salinity on the activities of Rubisco and RCA

Compared with the control, the activity of Rubisco did not change at 500 mM NaCl but increased at 200 mM NaCl when the seedlings were treated with salinity for 2 days. The activity of Rubisco increased significantly at 200 mM NaCl when the seedlings were treated with salinity for 14 days (Fig. 5a). The values at 200 and 500 mM NaCl were 1.28- and 1.10-fold higher than that at 0 mM NaCl, respectively (Fig. 5a).

The activity of RCA decreased at 500 mM NaCl compared with those under control conditions when the seedlings were treated with salinity for 2 days, while 200 mM NaCl did not affect the activity of RCA. When the seedlings were treated with salinity for 14 days, the activity of RCA increased at 200 mM NaCl but decreased at 500 mM NaCl (Fig. 5b). The values at 200 and 500 mM NaCl were 1.24- and 0.80-fold those at 0 mM NaCl, respectively (Fig. 5b).

4. Discussion

Soil salinization affects approximately 6% of the world's land area (Munns, 2005) and has a significant impact on plant growth, development, and reproduction among others (Flowers et al., 2010). Most plants are sensitive to salt stress during the germination of seeds and seedling establishment stages when the plants cannot tolerate severe environmental factors (Petrović et al., 2016). The seedlings grow slowly; the leaves wither, and photosynthesis decreases under salt stress (Munns, 2002). Morphological and physiological characteristics, such as biomass and leaf photosynthesis, can be used as important indicators to assess the

tolerance of plants to salt (Huang et al., 2012). In this study, the shoot dry weight increased at 200 mM NaCl when the seedlings were treated with salinity for 14 days (Fig. 1a), and the trend of Pn was the same as shoot dry weight (Fig. 1b). It conforms to a typically 'curvilinear' growth response to salt stress in halophytes, with peak growth at intermediate salinity (Ma et al., 2019). *S. salsa* has succulent leaves and is highly tolerant of salt; for example, it can effectively maintain ion homeostasis (Song and Wang, 2015). Therefore, seedlings may adapt to salinity when treated with NaCl for 14 days. As a result, the Pn increased at 200 mM NaCl compared with that under the control conditions (Fig. 1b). This indicates that 200 mM NaCl significantly promoted the ability of *S. salsa* to conduct photosynthesis, which may contribute to the increase in shoot dry weight under salinity.

Photosynthesis is the source of synthesis of organic matter and the accumulation of biomass in plants. The inhibition of photosynthesis under salt stress can be affected by stomatal and non-stomatal factors (Diao et al., 2014). The stomatal conductance of *S. glauca* was reduced under salt stress, but the intercellular CO₂ concentration did not decrease (Duan et al., 2018). This indicates that, in addition to stomatal factors, nonstomatal limitations, such as the chlorophyll content, ETR, and certain enzymes during carbon assimilation, may be key factors that affect the photosynthesis of plants under high saline conditions. Chlorophyll can absorb light energy and provides the starting power for photosynthesis (Lichtenthaler, 1987). The content of chlorophyll at 200 mM NaCl was significantly higher at 14 days than that at the control (Fig. 2). This indicates that the increased content of chlorophyll at 200 mM NaCl may have a positive effect on the Pn compared with that under control conditions (Fig. 1b).

The photochemical ability of PSII is an important indicator of photosynthesis, and PSII is highly sensitive to abiotic stress (Stepien and Johnson, 2009; Mathur et al., 2014). The maximal efficiency of PSII photochemistry (F_v/F_m) represents the maximum efficiency of the

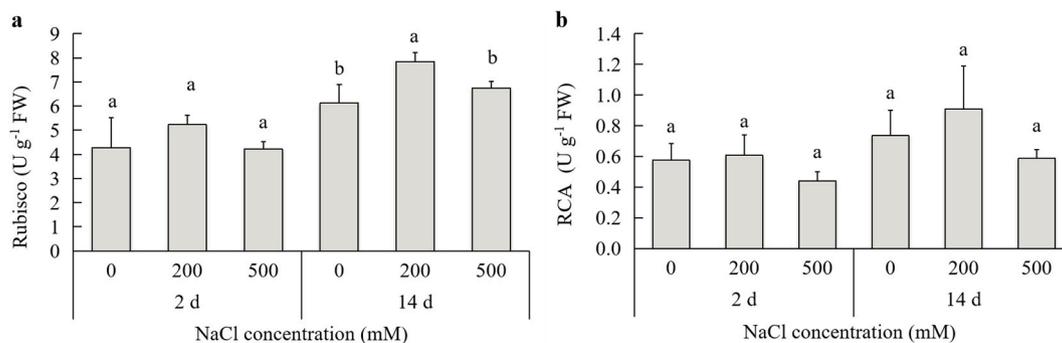


Fig. 5. Effect of salinity on the Rubisco (a) and RCA (b) activities of *Suaeda salsa*. The seedlings were treated with 0, 200, and 500 mM NaCl for 2 and 14 days. For each group of 3 bars at 2 or 14 days, the means with different letters are significantly different at $P < 0.05$. Vertical bars indicate the standard errors of means ($n = 3$).

utilization of light energy and reflects the structural and functional integrity of PSII of the optical system (Caffarri et al., 2014). The ETR reflects the rate of the non-linear electron transfer process in the optical system (Clarke and Johnson, 2001). Previous studies have shown that salinity can inhibit the ETR in *Arabidopsis* but promotes the ETR in *Thellungiella* (Stepien and Johnson, 2009). In this study, the F_v/F_m of *S. salsa* did not change under salinity during the entire time course, which indicates that the structure and function of PSII in *S. salsa* remain normal (Fig. 3a). The ETR increased with the increasing concentration of NaCl when the seedlings were treated with salinity for 14 days, and it was significantly enhanced by NaCl (Fig. 3b). This indicates that the photosystem of *S. salsa* can maintain its normal state, and the ETR of photosystem is more efficient under saline conditions.

The chloroplast FNR in plants catalyzes the transfer of electrons to $NADP^+$, which is the last step of the photosynthetic linear electron transport chain (Lu et al., 2003). Drought stress leads to the readily apparent release of FNR in thylakoid membranes, which causes a reduction in the $NADP^+$ photoreduction ability (Mulo, 2011). In this experiment, the FNR activity gradually increased with the increase in concentration of NaCl at 14 days (Fig. 4a). Similarly, the level of NADPH gradually increased when the seedlings were treated with salinity (Fig. 4b). This indicates that the photoreaction system of *S. salsa* may be enhanced to some extent when the seedlings were treated with salinity. These findings merit further verification.

The Calvin cycle is a key pathway for plant energy and carbon metabolism, and Rubisco is the rate-limiting enzyme in the Calvin cycle. Rubisco is the most abundant soluble protein in plants, accounting for approximately 50% of the total soluble protein in plants, but its catalytic efficiency is very low (Parry et al., 2003). RCA plays an important role in controlling the initial activity of Rubisco and Pn in rice (Jiang et al., 2000). The activities of Rubisco and RCA increased when the seedlings were treated with salinity for 14 days, particularly for the activity of Rubisco at 200 mM NaCl (Fig. 5). It has been regarded that limitation in the content or activity of Rubisco is one of the most important biochemical factors involved in the salt-related down-regulation of photosynthesis (He et al., 2014). Salt stress can induce the formation of chloroplast protrusions (CP), which are the early stages of formation of Rubisco-containing bodies (RCBs), indicators of Rubisco degradation (He et al., 2014). The average number of CPs and RCBs per chloroplast or cell in the salt-sensitive soybean cultivar Melrose was greater than that in the salt-tolerant soybean S111-9 under salt stress. Moreover, salt stress reduced the initial and total activities of Rubisco by 22% and 45% in Melrose, respectively, and only 6% and 21% in S111-9, respectively (He et al., 2014). This indicates that lower formation of CPs and RCBs, which indicates a higher content or activity of Rubisco, could be one of the important mechanisms for the resistance of plants to salt (He et al., 2014). In this study, 200 mM NaCl increased the activity of Rubisco, while 500 mM NaCl did not decrease it (Fig. 5a). This indicates that maintaining stable Rubisco activity could correlate with the high ability of the euhalophyte *S. salsa* to tolerate salt. In this study, salinity did not improve the value of all parameters during photoreaction and carbon assimilation stages during the initial 2 days. However, 200 mM NaCl promoted the value of all photosynthetic parameters, particularly the activity of Rubisco, chlorophyll content and Pn, when the seedlings were treated with NaCl for 14 days. Moreover, 500 mM NaCl had no adverse effects on those parameters. This indicates that this species does not suffer from the ion-specific effect of high salinity, and some concentrations of ions that accumulate in the leaves (chloroplasts) can even promote photosynthetic capacity in *S. salsa*. The mechanism of positive effect of NaCl on photosynthesis merits further study.

In conclusion, the results of this study reveal that NaCl can improve the chlorophyll content, ETR, and level of NADPH, and the activities of FNR, Rubisco and RCA, particularly the activity of Rubisco and chlorophyll content, when the seedlings were treated with 200 mM NaCl. This indicates that the ability to absorb light, transfer energy from the photosynthetic system and assimilate carbon can be enhanced at

treatment with 200 mM NaCl, which could explain why *S. salsa* produces the highest biomass at approximately 200 mM NaCl.

Author contributions

Qiang Li and Ru Liu performed the experiment and analyzed the data with Zihan Li. Qiang Li and Ru Liu wrote the paper. Hai Fan and Jie Song designed the experiments and revised the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.plaphy.2022.02.019>.

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