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RESEARCH PAPERS

Effects of Salt Stress on Photosynthetic Pigments and Activity of Ribulose-1,5-bisphosphate Carboxylase/Oxygenase in *Kalidium foliatum*[1]

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Abstract—The effects of NaCl and Na_2SO_4 on photosynthetic pigments, malondialdehyde (MDA), Rubisco activity and superoxide dismutase (SOD) activity were investigated in *Kalidium foliatum* (Pall.) Moq., which is distributed in the saline soil of Hetao irrigation area in Inner Mongolia China. The *K. foliatum* plants were treated with NaCl (0, 100, 250, 400 and 500 mM), Na_2SO_4 (0, 100, 250, 400 and 500 mM) and NaCl + Na_2SO_4 (1 : 1, v/v) (0, 100, 250, 400 and 500 mM of Na^+ concentration, 0, 50, 125, 200 and 250 mM of $Cl^-$and SO_4^{2-} concentration) for 10 days. Content of chlorophylls and carotenoids were significantly higher than control at increasing NaCl and Na_2SO_4 concentration, in contrast, were significantly reduced by higher concentration of NaCl + Na_2SO_4. Rubisco activity reduced steadily at 100 and 250 mM NaCl, while increased at 400 and 500 mM NaCl. Rubisco activity was significantly higher than control at 100 mM Na_2SO_4, and was no more change under NaCl + Na_2SO_4 treatment. The SOD activity increased with increasing NaCl and Na_2SO_4, and increased at moderate NaCl + Na_2SO_4 treatment. MDA content was lower than control at 250 mM salt concentration. On the basis of the data obtained, *K. foliatum* showed resistance to salt such as Na^+, $Cl^-$and SO_4^{2-}, Rubisco activity in *K. foliatum* might be more sensitive to salt.

Keywords: Kalidium foliatum, halophyte, photosynthetic pigment, malondialdehyde, Rubisco, superoxide dismutase, salt treatment

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INTRODUCTION

Salt stress is a major environmental factor limiting plant growth and development globally [1]. Salinity often causes water deficiency and ion toxicity that inhibits plant growth by disrupting physiological processes, especially photosynthesis [2]. The primary function of photosynthetic pigments in plants is photosynthesis. Chlorophyll pigments help leaves capture light energy. Chlorophyll and carotenoids are central to energy acquisition for green plants, and significant changes in their concentrations cause marked effects on the entire process of plant metabolism [3].

Salt stress induces photosynthesis inhibition through the reduction of Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco, EC 4.1.1.39) activity, photosynthetic pigment loss, and degradation of membrane proteins in photosynthetic apparatus [4]. Ribulose-1,5-bisphosphate carboxylase/oxygenase is a bifunctional enzyme located in the stroma of chloroplast. It catalyses CO_2 fixation to ribulose-1,5-bisphosphate (RuBP) and is the first step of photorespiration [5]. Studies have shown that salt stress affects photosynthesis by limiting the content or activity of Rubisco [6]. The decrease of Rubisco content or activity has been shown to cause low carboxylation efficiency in salt-sensitive soybean [7].

In living organisms, reactive oxygen species (ROS) are produced as a result of stress conditions. ROS molecules include free radicals such as hydroxyl radical (•OH), superoxide ($O_2^{\bullet-}$), and non-radical molecules like hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$). Superoxide dismutase (SOD) converts superoxide radical to H_2O_2, while ascorbate peroxidase (APX) catalyses the conversion of H_2O_2 to water and oxygen [8], Neto et al. reported that SOD increased in the leaves of salt-tolerant and salt-sensitive maize cultivars under salt stress, and the increase in the activity of

[1] The article is published in the original.

Abbreviations: Chl—chlorophyll; Rubisco—ribulose-1,5-bisphosphate carboxylase/oxygenase; RuBP—ribulose-1,5-bisphosphate; SOD—superoxide dismutase.

Table 1. The soil ions in the sampling area

		Depth of soil, cm		
		0–20	20–40	40–60
pH		6.333	6.533	6.467
Cation, g/kg	Na^+	2.445	0.457	0.224
	K^+	0.328	0.342	0.026
	Ca^{2+}	0.259	0.317	0.130
	Mg^{2+}	0.156	0.075	0.031
Anion, g/kg	Cl^-	3.125	0.563	0.100
	SO_4^{2-}	2.132	1.732	0.379
	HCO_3^-	0.316	0.063	0.581
	NO_3^-	0.008	0.011	0.039

Table 2. The type and concentration of salt

Type of salt	Concentration of salt, mM				
NaCl	0	100	250	400	500
Na_2SO_4	0	100	250	400	500
NaCl + Na_2SO_4 (1 : 1)	0	100	250	400	500

antioxidant enzymes is greater in the salt-tolerant cultivar than in the salt-sensitive one [9].

Malondialdehyde (MDA) is one of the final decomposition products in membrane lipid peroxidation. MDA is one of the most commonly used biomarkers of oxidative stress, and is described as a damage indicator [10]. The rate of toxic oxygen species production surpassing the rate of its scavenging will lead to the accumulation of activated oxygen species, and will consequently lead to a higher MDA content [11]. Xue and Liu [12] reported that NaCl treatment causes a significant increase in MDA levels of leaves, indicating a high rate of lipid peroxidation due to salt stress. MDA has widely been utilized to differentiate salt-sensitive and salt-tolerant crop cultivars [12].

Halophytes are tolerant plant species to highly salinity conditions, and different strategies have been developed to survive and complete their life cycles in such a harsh salt soil environment. *Kalidium foliatum* is a halophyte in the family Chenopodiaceae, which is resistant to salt. At present, there is little research about the effects of stress induced by salt stress on *K. foliatum*. Soil salinity has a negative effect on plant growth. In inland arid saline soil, salt composition is complex. The soils are generally composed by a mixture of different salt species among which sulfate and chloride are often the most abundant. The effects of the salt mixtures on plant physiology are different than those caused by simple salt [13]. The aim of this work was to determine the effects of simple salt (NaCl or Na_2SO_4) and salt mixtures (NaCl + Na_2SO_4) on the content of photosynthetic pigments, activity of Rubisco and superoxide dismutase, malondialdehyde in the leaves of *K. foliatum*.

MATERIALS AND METHODS

Plant material and growth conditions. *Kalidium foliatum* (Pall.) Moq. seeds were collected from an area in Bayannaoer City, Inner Mongolia, China. The soil in the area is considered strongly saline, and pH is 6.2–7.0. The major cation in the soil was Na^+, and the major anion was Cl^- and SO_4^{2-} (Table 1). *K. foliatum* seeds were treated with sublimate for 8 minutes and washed with distilled water to remove the sublimate. The seeds were cultured in a cultivation cabinet at 27°C for 2 days keeping them fully watered until the beginning of the germination. A mixture of soil and composting sheep manure in the ratio of 5 : 1 was mixed with vermiculite at the ratio of 3 : 1 to increase soil permeability. The mixed soils were put into nutritive pots, the germinating seeds were planted into the nutritive pots and grew for 4 months at 25/15°C day/night temperature, under 14 h photoperiod (light intensity 5000 lux). The Seedlings were irrigated with 30 mL distilled water every two days during this period.

Salt treatment. All plant materials were treated with different salt concentrations to monitor stress (Table 2). Each pot was watered with 30 mL the various saline solutions until soil saturation. Evaporated water was replenished with distilled water every 2 days. The photosynthetic pigments, the activity of Rubisco and superoxide dismutase, MDA were measured after salt treatment for 10 days.

Measurements of photosynthetic pigment. The photosynthetic pigments of the plants in each treatment were extracted using 0.1 g of fresh material in 80% acetone according to Lichtenthaler [14]. Chlorophyll was extracted from the leaves collected for chlorophyll fluorescence by cutting every leaf (0.1 g) into pieces in a mortar with a mixture of SiO_2, $CaCO_3$ and 80% (v/v) acetone. Leaf pieces were then soaked for 5 min in darkness. Chlorophyll and carotenoid contents were determined with a Microplate reader (Gene Company, Hong Kong). The concentrations of the pigments were calculated according to the formula provided by Yang et al. [15]:

$$\text{Chl } a \text{ (mg/g fr wt)} = [(12 \times A_{663}) - (2.69 \times A_{645})]V/1000W, \quad (1)$$

$$\text{Chl } b \text{ (mg/g fr wt)} = [(22.9 \times A_{645}) - (4.68 \times A_{663})]V/1000W, \quad (2)$$

$$\text{total Chl (mg/g fr wt)} = [(20.2 \times A_{645}) + (8.02 \times A_{663})]V/1000W, \quad (3)$$

$$\text{carotenoids (mg/g fr wt)} = [(7.6 \times A_{440}) - (20.21 \times A_{645} + 8.02 \times A_{663})]V/1000W, \quad (4)$$

where A is optical density at the respective wavelength, V is the final volume of Chl extract in 80% acetone, and W is fresh weight of tissue extracted.

Assay of Rubisco activities. Rubisco activity was determined at 340 nm using a spectrophotometer (U2910, Hitachi, Japan). Rubisco was extracted according to Chen et al. [16]. 2.0 g of frozen *K. foliatum* leaf discs were ground with a pre-cooled mortar and pestle with liquid nitrogen in 1 mL of extraction buffer containing 100 mM Tris (pH 7.6), 10 mM $MgCl_2$, 2 mM ethylenediamine tetraacetic acid (EDTA), 10 mM $NaHCO_3$, 10 mM β-mercaptoethanol. The extract was centrifuged at 15000 rpm for 10 min in 4°C. After purification and drying, the supernatant was added to 1 mL of vitality test liquid containing 100 mM Tris-HCl (pH 8.2), 10 mM $NaHCO_3$, 20 mM $MgCl_2$, 1 mM DTT, 0.5 mM NADH, 5 mM ATP and was used immediately for the assay of Rubisco activity.

Rubisco activity was determined according to Lin et al. [17]. For initial activity, 100 μL of inactive enzyme extraction buffer was added to the sample extract of the assay solution. One unit of NAD-glyceraldehyde-3-phosphate dehydrogenase and one unit of 3-phosphoglyceric phospokinase were immediately added and mixed well. The change in absorbance at 340 nm was monitored for 1 min using a microplate reader (BioTek Synergy HT Multi-Mode Microplate Reader, United States). For total activity, 100 μL of 1.35 mM ribulose-1,5-bisphosphate (RuBP) was added and mixed well. The change of absorbance at 340 nm was monitored for 2 min and measured for every 15 s. Rubisco activation state was calculated as the ratio of initial activity to total activity.

Measurements of superoxide dismutase activity. Superoxide dismutase was determined in leaves using Tris-HCl. 0.15 g leaves were collected by cutting leaf into pieces in a mortar with 50 mM Tris-HCl for 10 min at 4°C. The extract was centrifuged at 1000 rpm for 15 min in 4°C. The supernatant was in 2.9 mL of vitality extracting solution containing 14.5 mM D-methionine, 3 μM EDTA, 2.25 mM nitro blue tetrazolium chloride, 60 μM riboflavin, and was used immediately for the assay of superoxide dismutase activity. After mixing well under light for 10 min, SOD activity was estimated from optical density value at wavelengths of 560 nm using a microplate reader (BioTek Synergy HT Multi-Mode Microplate Reader, United States). The activity of SOD was expressed as U/g of leaves.

Measurements of malondialdehyde content. MDA content was determined following thiobarbituric acid method according to Islam et al. [18]. Approximately 0.2 g leaves preserved in liquid nitrogen were homogenized in 3 mL of 10% trichloroacetic acid (TCA), then centrifuged at 4000 rpm for 10 min, after which 2 mL of 0.6% thiobarbituric acid (TBA) in 10% TCA was added to an aliquot of 2 mL of supernatant. The mixture was heated in boiling water (92°C) for 15 min, and then quickly cooled in an ice bath. After centrifugation at 1800 rpm for 10 min, the absorbance of the supernatant was determined at 450, 532 and 600 nm using a spectrometer (U2910, Hitachi, Japan). The concentrations of the MDA were calculated according to the formula:

$$\text{MDA (μmol/g fr wt)} = [6.452 \times (A_{532} - A_{600}) - 0.559 \times A450]V/(W_o \times V_o),$$

where A is optical density at the respective wavelength, V is the total extraction volume, W_o is fresh sample weight, and V_o is sample volume.

Statistical analysis. All experiments were performed in triplicate. The data determined in triplicate were visualized with CIAS2.0 and Origin 8.6. Individual differences among means were determined by a Duncan's test. Before *ANOVAs*, data were checked for normality and homogeneity of variance, and log-transformed to correct deviations from these assumptions when needed. Statistical analyses were conducted with the software package SPSS 19.0. P-value < 0.05 was considered significant.

RESULTS

Chlorophyll and Carotenoid Contents

Photosynthesis, the primary step to energy production, is inhibited by salt stress, through affecting chlorophyll and carotenoids. Salt stress increased the activity of chlorophyllase, which promoted degradation of chlorophyll, reduced chlorophyll content with increased level of salt stress [19]. Although salt stress reduces the chlorophyll content, the extent of the reduction depends on salt tolerance of plant species. So the chlorophyll has been proposed as one of the biochemical indicators of salt tolerance in different plants [20]. Carotenoids play an important role as a precursor in signaling during the plant development under abiotic stress. Carotenoids protect the membranes from oxidative damage [21]. Our data that photosynthesis pigments were significantly higher than control with the 250 mM NaCl treatment and with 100 and 400 mM Na_2SO_4. The change in chlorophyll *b* content was not significant under different salt treatment, while the content of chlorophyll *a* and carotenoids differed significantly between different salt concentrations (Fig. 1). One possible explanation for this result may be that *K. foliatum* is a halophyte species which showed a tolerance to higher salt.

Rubisco Carboxylation Enzyme Activity

As the key regulatory and rate limiting enzyme of CO_2 assimilation, ribulose-1,5-bisphosphate carboxylase (Rubisco) plays a central role in photosynthesis [22]. Salinity leads to the decrease of Rubisco activity and the rapid inhibition of photosynthesis [23]. The increase in the amount of Rubisco can be beneficial for the survival of plants under harsh environmental

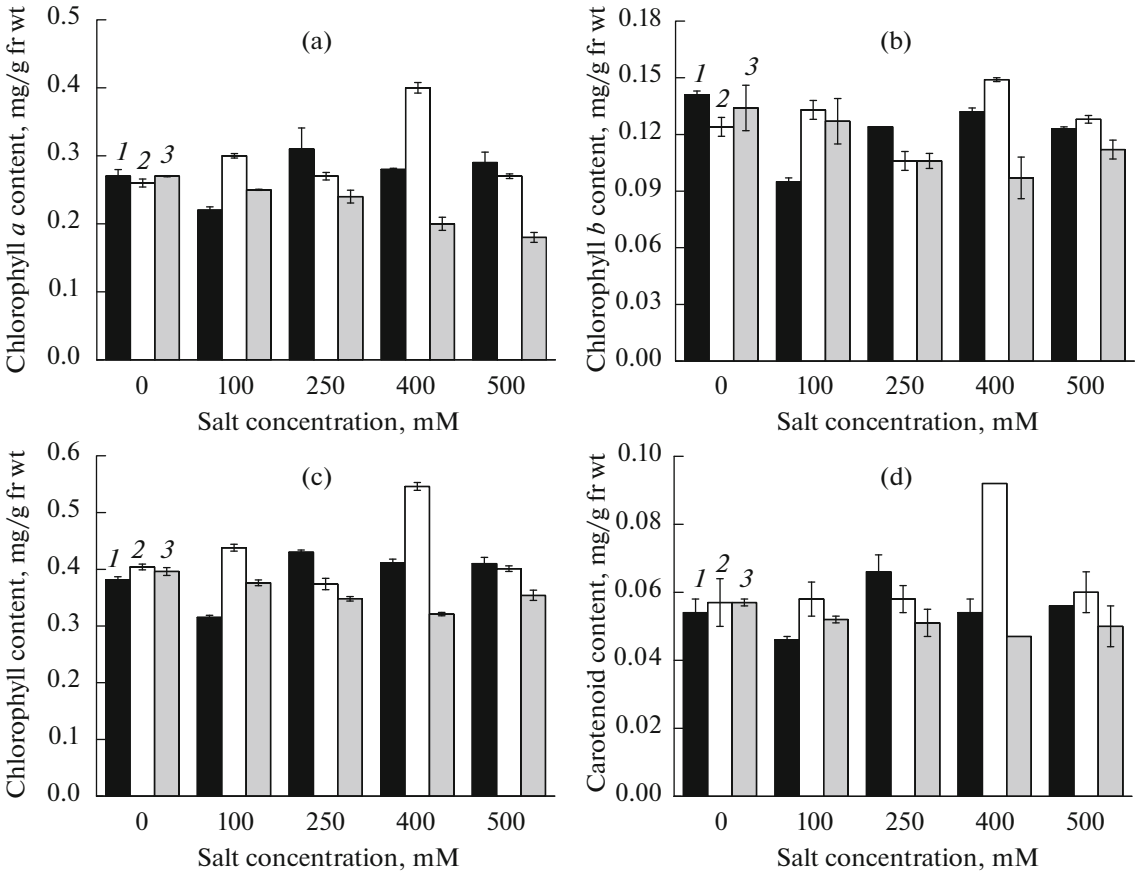

Fig. 1. Effects of different salt treatment on photosynthetic pigments of *Kalidium foliatum* leaves: (a) chlorophyll *a*; (b) chlorophyll *b*; (c) total chlorophyll; (d) carotenoids. *1*—NaCl; *2*—Na_2SO_4; *3*—NaCl + Na_2SO_4.

conditions. Aragão et al. [24] reported that Rubisco activity decreased more markedly in salt-sensitive cultivar than in salt-tolerant cultivar of *Vigna unguiculata*. Our study discovered that Rubisco activity of *K. foliatum* is no more changes under NaCl and NaCl + Na_2SO_4 treatment, conversely, significant changes in Rubisco activity were observed in the range of 100–500 mM Na_2SO_4 treatment for *K. foliatum* (Fig. 2). Our results clearly indicate that *K. foliatum* is tolerant to NaCl and NaCl + Na_2SO_4 treatment, and *K. foliatum* have a capacity to adapt to salt salinity such as Na^+, Cl^- and SO_4^{2-}.

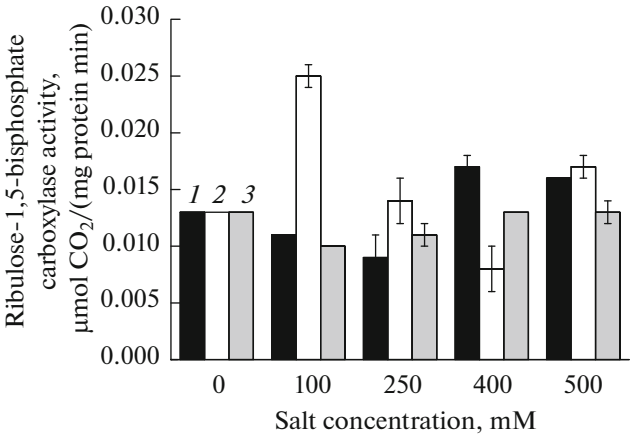

Fig. 2. Effects of different salt treatment on ribulose-1,5-bisphosphate carboxylase of *Kalidium foliatum* leaves. *1*—NaCl; *2*—Na_2SO_4; *3*—NaCl + Na_2SO_4.

Superoxide Dismutase Activity

Increased salinity brings to oxidative damage due to increased production of reactive oxidative damage (ROS) [25]. Plants were induced to synthetize antioxidant enzymes to maintain the normal growth of plant. Superoxide dismutase (SOD) is one of the crucial enzymes that protect plant against the ROS damages [26]. Agarwal and Pandey [27] found that less membrane damage and higher activity of SOD in *C. angustifolia*, which were correlated with higher salinity tolerance. The induction of low salt concentrations for SOD activities was an adaptive reaction of plant for salt treatment to enhance the ability of eliminating ROS, the inhibition of high salt concentrations for SOD activities can be thought that the tolerance of

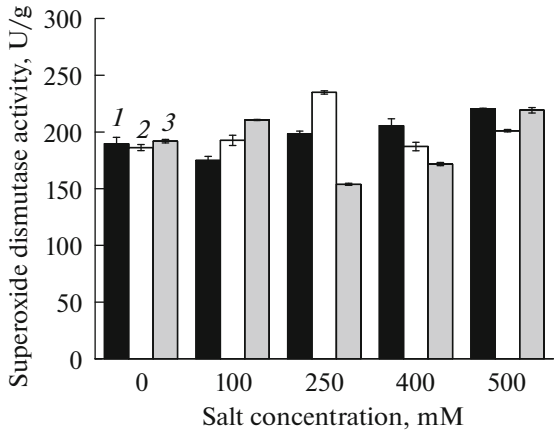

Fig. 3. Effects of different salt treatment on superoxide dismutase (SOD) of *Kalidium foliatum* leaves. *1*—NaCl; *2*—Na_2SO_4; *3*—NaCl + Na_2SO_4.

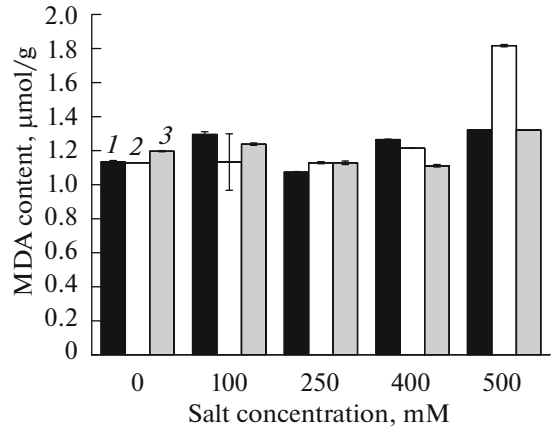

Fig. 4. Effects of different salt treatment on malondialdehyde (MDA) of *Kalidium foliatum* leaves. *1*—NaCl; *2*—Na_2SO_4; *3*—NaCl + Na_2SO_4.

plant for salt stress has exceeded itself adaptability [28]. The data in our study indicate that the SOD activities in *K. foliatum* leaves increased under low salt concentrations, while higher-dose NaCl treatment resulted also in an increase in the SOD activities (Fig. 3). These results suggest that *K. foliatum* might show a high capacity of eliminating ROS for adapting to NaCl treatment. This adaptation can be seen as a survival mechanism of *K. foliatum* to saline environments in the evolutionary process.

Malondialdehyde Content

Salt treatment leads to oxidative stress [29], which causes increased MDA content in plants. The amount of malondialdehyde (MDA) reflects lipid peroxidation levels in plants exposed to salt stress [29]. MDA is usually used to evaluate the status of the osmotic adjustment, which is important in the adaptation of plants to environmental stress. Lower MDA displays a higher anti-oxidative ability, which reflects a higher stress resistance [30]. The change of MDA content in *K. foliatum* showed a small change under NaCl and Na_2SO_4 treatments, suggesting that *K. foliatum* is better protected against oxidative damage under salt treatment. The small changes can be seen as a smaller damage to cellular membranes due to lipid peroxidation as indicated by lower accumulation of MDA. 500 mM Na_2SO_4 treatment led to the highest MDA content, which indicated that *K. foliatum* has poor tolerance to high concentration of Na_2SO_4. However, 500 mM NaCl + Na_2SO_4 treatment led to the lower MDA content, which indicated that *K. foliatum* could be more tolerant to high concentration of Na^+, Cl^- and SO_4^{2-} than Na^+, Cl^- or Na^+, SO_4^{2-} separately (Fig. 4).

Taken together, *K. foliatum* exhibit a higher photosynthesis pigment, Rubisco and SOD activities, and show a lower MDA content in response to NaCl and Na_2SO_4 treatment. *K. foliatum* was capable of adapting to different salt treatment, especially NaCl, and low salt concentrations are beneficial to *K. foliatum*.

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