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Full Length Article

Protective Effect of Cerium against Salinity-Induced Oxidative Stress in Jerusalem Artichoke (*Helianthus tuberosus*)

Wenjun Li[1], Zhihong Tang[2*], Jiasen Lv[2], Bao Ju[2], Zhengyi Liu[1] and Song Qin[1*]
[1]*Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai 264003, China*
[2]*College of Life Science, Yantai University, Yantai 264005, China*
[*]For correspondence: tangzhihong7405@163.com; sqin@yic.ac.cn

Abstract

The effects of cerium (Ce) on protecting Jerusalem artichoke (*Helianthus tuberosus* L.) against oxidative stress induced by salinity were studied. Exposure to NaCl (150 m*M*) markedly inhibited the growth of *H. tuberosus* seedlings and the inhibition was significantly alleviated by $CeCl_3$ (0.1 m*M*). The result showed that $CeCl_3$ prevented decline in the chlorophyll content induced by salinity. The contents of hydrogen peroxide (H_2O_2), superoxide radicals ($O_2^{\cdot -}$) and malondialdehyde (MDA) were increased, which suggested that oxidative stress induced by salinity. Addition with $CeCl_3$ dramatically depressed H_2O_2, $O_2^{\cdot -}$ and MDA accumulation caused by salt stress. Furthermore, the activities of superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD) in *H. tuberosus* seedlings under salt stress were also increased. The data suggested that appropriate concentration $CeCl_3$ could protect *H. tuberosus* from salinity-induced oxidative stress by reducing cellular level of ROS directly and by improving antioxidant defense system.

Keywords: Jerusalem artichoke; Cerium; Salinity; Oxidative stress; Antioxidant defense system

Introduction

Soil salinity influences plant productivity around the globes (Shabala and Cuin, 2008). In plants, salt stress causes adverse effects on energy production, photosynthesis, lipid metabolism and so on (Wu *et al*., 2014; Kasim *et al*., 2016; Tabassam *et al*., 2016). Moreover, salt stress results in oxidative stress by increasing in cellular level of reactive oxygen species (ROS) (Mittler, 2002; Nounjan *et al*., 2012). These ROS are highly reactive molecules which cause protein denaturation, DNA mutation and lipid peroxidation thereby bringing about cellular damage (Tanou *et al*., 2009). To alleviate oxidative injury plants have executed different kinds of antioxidant activities including catalase (CAT, EC1.11.1.6), peroxidase (POD, EC 1.11.1.7), superoxide dismutase (SOD, EC 1.15.1.1), glutathione (GSH) and ascorbate (AsA), which have the ability to detoxify ROS (Ashraf and Ali, 2008; Ashraf, 2009; Sergio *et al*., 2012).

The rare earth elements (REEs) are a set of seventeen trivalent metallic elements (Liu *et al*., 2012). A large quantity of REEs have entered into the environment and accumulated in the ecosystem. For instance, cerium (Ce) nitrate has been widely used as a microelement fertilizer for improving agricultural productivity in China (Wang *et al*., 2012; Zhang *et al*., 2013). Low concentrations of Ce^{3+} had positive effects for *A. flosaquae*. The optimum concentration Ce^{3+} was 0.1 mg/L. High concentrations of Ce^{3+} led negtive effects to *A. flosaquae*. Exposure to high concentrations of Ce3+led todecrease of Chla content (Wang *et al*., 2012). Ce^{3+} application could reduce ROS and malondialdehyde (MDA) contents and decrease cell membrane permeability of spinach (Liao *et al*., 1994; Hong *et al*., 2002). Although numerous physiological effects of cerium on plants have been reported in recent years, the essentiality of cerium on plants exposed to environmental stresses is still largely unknown.

Jerusalem artichoke (*Helianthus tuberosus* L.) is an economically important crop species (Monti *et al*., 2005). It is not only as a food for human consumption but also has numerous industrial uses (Long *et al*., 2008; Huang *et al*., 2012). Previous research has indicated that a high oxidative damage and suppressed antioxidant defense system of *H. tuberosus* exposed to salt stress (Xue and Liu, 2008). Up to now, there is no information known about the influence of cerium on oxidative stress in this plant under salt stress. In the present study, the effect of cerium on the growth and antioxidative defense system in *H. tuberosus* seedlings exposed to salt stress was investigated. The aim of the present study was to evaluate the role of cerium in the alleviation of negative effects of salinity on *H. tuberosus* seedlings.

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Materials and Methods

Plants and Treatments

Jerusalem artichoke (*Helianthus tuberosus* L.) N1 was selected for this study from Tai'an Blue Source Agricultural Co. Ltd. Shandong province, China. All the experiments were carried out in a greenhouse. The minimum and maximum temperatures were 21 and 31ºC, respectively. Tuber slices with buds of N1 were sown in 20-mesh quartz sand. After 20 days, uniform size seedlings were planted into 4 L plastic pots containing quartz sand (Wang *et al*., 2011a).

Five days later, the plants were divided into five groups as follows: control group (marked as Control), treated with half-strength Hoagland solution; Salt stress group (marked as NaCl), treated with 150 m*M* NaCl in half-strength Hoagland solution; $CeCl_3$-treated groups (marked as Ce), treated with $CeCl_3$ (0.1 m*M*) in half-strength Hoagland solution; NaCl with supplemental $CeCl_3$ (marked as Ce+NaCl), treated with $CeCl_3$ (0.1 m*M*) and NaCl (150 m*M*) in half-strength Hoagland solution. The treatment concentrations were based on previous studies, in which a number of lower and higher levels of $CeCl_3$ were applied. Plants were harvested for biochemical and physiological analyses after 15 days of treatment.

Plant Growth Measurement

The height and fresh weights of the plants were recorded. Then a known amount of homogenized samples was incubated in an oven at 70ºC until there were no further changes and dry mass was determined.

Chlorophyll Contents Measurements

Total chlorophyll in leaves were extracted and measured according to Wellburn (1994). Chlorophyll was extracted with chilled 80% (v/v) acetone in the dark. The extract was centrifuged at 5,000 g for 5 min and then the supernatant was analyzed spectrophotometrically at 646 and 663 nm for chlorophyll.

Assay of H_2O_2, $O^{\cdot}{}_2^-$ and MDA Levels

Leaves collected from the plants were homogenized in chilled phosphate buffer (50 m*M*, pH7.8) containing 1% (v/v) polyvinylpyrrolidone, 5 m*M* ethylenediaminetetraacetic acid and 5 m*M* dithiothreitol. The homogenates were centrifuged at 12 000 g for 20 min at 4ºC and the supernatants were used for assays of H_2O_2, $O_2{\cdot}^-$ and MDA levels and enzymatic activities.

H_2O_2 content was measured at 390 nm (Wang *et al*., 2009). The $O_2{\cdot}^-$ was determined at 530 nm by measuring the content of nitrite (Elstner and Heupel, 1976). Lipid peroxidation was assayed by measuring MDA content using the thiobarbituric acid (TBA) reaction (Buege and Aust, 1978).

Measurements SOD, POD and CAT Activities

The activity of SOD was assayed by measuring the ability to inhibit photochemical reduction of nitroblue tetrazolium (NBT) (Beauchamp and Fridovich, 1971). One unit of SOD activity was equated to the amount of enzyme required to cause 50% inhibition in the rate of NBT photo reduction. CAT activity was determined by following the decomposition of H_2O_2 at 240 nm (Durner and Klessing, 1996). 1 μM H_2O_2 decomposed in one minute was equated to one unit of CAT. The activity of POD was assayed by the increase per minute in the absorbance at 470 nm during the oxidation of guaiacol according to Hammerschmidt *et al.* (1982). One unit of POD activity was equated to an increase of 0.01 absorbance units per minute.

Statistical Analysis

The experiments were repeated three times. Based on the appropriate two-way variance analysis (ANOVA) the analysis of variance was computed for statistically significant differences determined. SPSS software (SPSS Inc., version 18.0, Chicago, USA) was used to perform statistical analysis, followed by the Duncan's Multiple Range Test (DMRT). All measured data were expressed as mean ± SD. Differences between treatment and comparisons with $P<0.05$ were considered as statistical significance.

Results

Growth of *H. Tuberosus* Plant

Table 1 shows the plant height, fresh weight and dry weight of *H. tuberosus* seedlings under various conditions. Under NaCl (150 m*M*) treatment, the plant height, fresh weight and dry weight were significantly decreased by 45.2, 36.8 and 32.1%, respectively compared to the control seedlings. However, application of 0.1 m*M* $CeCl_3$ to the saline nutrient solution, the plant height, fresh weight and dry weight were significantly increased by 24.4, 26.9 and 33.8%, respectively. Under normal condition, the application of 0.1 m*M* $CeCl_3$ obviously improved the plant height, fresh weight and dry weight of the seedlings.

Chlorophyll Content

The effects of various treatments on the contents of chlorophyll a (chl-a), chlorophyll b (chl-b) and total chlorophyll are shown in Table 2. When compared with the control group, the 150 m*M* NaCl treatments significantly decreased chl-a, chl-b and total chlorophyll contents by 40.2, 53.8 and 46.3%, respectively. However, NaCl-induced reduction in chl-a, chl-b, total chlorophyll content was alleviated by 0.1 m*M* $CeCl_3$ addition, significantly increased them by 43.1, 72.2 and 54.3%.

Table 1: Effect of $CeCl_3$ and NaCl on growth indexes of *H. tuberosus*

Growth parameters	Treatment			
	Control	NaCl	Ce	NaCl + Ce
Fresh weight (g)	10.71±0.35ab	5.08 ± 0.26d	11.52 ± 0.39a	7.15 ± 0.12c
Dry weight (g)	1.06±0.07b	0.67±0.04d	1.21 ± 0.26a	0.85 ± 0.17bc
Plant height(cm)	19.35±0.76ab	11.61±0.43d	20.26 ± 0.85a	15.53 ± 0.59c

Each value represents the mean ± SD, n=3. Different letters within each each column indicate statistically significant differences at $P<0.05$ using Duncan's Multiple Range Test (DMRT)

Table 2: Effect of $CeCl_3$ and NaCl on chlorophyll contents of *H. tuberosus*

Chlorophylls	Treatment			
	Control	NaCl	Ce	NaCl + Ce
chl-a content (mg g^{-1} FW)	0.97±0.05b	0.58±0.02d	1.12 ± 0.04a	0.83 ± 0.03c
chl-b content (mg g^{-1} FW	0.78±0.03ab	0.36±0.01d	0.85 ± 0.02a	0.62 ± 0.02c
Chl(a+b) content (mg g^{-1} FW)	1.75±0.06b	0.94±0.03d	1.97 ± 0.06a	1.45 ± 0.04c

Each value represents the mean ± SD, n=3. Different letters within each each column indicate statistically significant differences at $P<0.05$ using Duncan's Multiple Range Test (DMRT)

The result suggested that 0.1 m*M* $CeCl_3$ application increased the content of chl-b more significantly than the other two indicators of seedlings under salt stress. Furthermore, under normal condition 0.1 m*M* $CeCl_3$ application notably enhanced chl-a, chl-b and total chlorophyll contents of *H. tuberosus*.

ROS Accumulation and Lipid Peroxide Level

The contents of H_2O_2, $O_2^{\cdot -}$ and MDA in *H. tuberosus* seedlings under various conditions were shown in Fig. 1. It can be seen that H_2O_2, $O_2^{\cdot -}$ and MDA contents of *H. tuberosus* seedlings increased in response to 150 m*M* NaCl stress compared to the control. H_2O_2 contents of the seedlings treated by NaCl were significantly increased and being 49.3% higher than that of control. However, 0.1 m*M* $CeCl_3$ addition significantly diminished H_2O_2 content (about 23.2%) in NaCl treatment. NaCl treatment brought about a sharp $O_2^{\cdot -}$ accumulation up to approximately double of the control but inhibited about 15.9% by $CeCl_3$ addition. NaCl stress caused a 60.7% increase in the MDA content of seedlings in controls. However, at the same NaCl concentration 0.1 m*M* $CeCl_3$ application significantly reduced the seedlings MDA content (about 21.9%) compared with those of NaCl treatment. Under normal condition $CeCl_3$ application showed no significant increases H_2O_2, $O_2^{\cdot -}$ and MDA contents of the seedlings.

Antioxidant Defense

The effects of different treatments on SOD, CAT and POD activities are presented in Fig. 2. The activity of SOD in leaves of *H. tuberosus* seedlings treated by 150 m*M* NaCl was significantly increased compared with the control. The application of 0.1 m*M* $CeCl_3$ to NaCl-treatment solutions increased the activities of SOD by 39.7% compared with the plants treated with NaCl. CAT activity in leaves of NaCl-treatment *H. tuberosus* seedlings was relatively low compared with the control. However, addition of 0.1 m*M* $CeCl_3$ to NaCl-treatment solutions stimulated the activity of CAT (about 31.9%) in the leaves. The activity of POD in NaCl-stressed leaves, significantly increased compared with the control. Similar to the effect on the activity of SOD the addition of 0.1 m*M* $CeCl_3$ to NaCl-treatment solutions enhanced POD activity by 23.9% in leaves of NaCl-treatment plants. The result indicated that treatment with $CeCl_3$ (0.1 m*M*) increased SOD activity more significantly than CAT and POD activities of seedlings under salt stress. Under normal conditions the application of 0.1 m*M* $CeCl_3$ seemed to be no notable effects on SOD activity but obviously enhanced CAT and POD activities of the seedlings compared to the control.

Discussion

The growth status of plant can be reflected by growth indices such as the plant height, fresh weight (leaves, stems and roots) and dry weight of plant (Ni *et al*., 1996). In the present study, treatment with NaCl (150 m*M*) significantly inhibited the plant height, fresh weight and dry weight of *H. tuberosus* seedlings. A growth reduction would be potential energy cost for salinity combat (Munns and Tester, 2008). The results from the present work indicate 0.1 m*M* $CeCl_3$ application significantly improved the growth of seedlings grown under salt stress. It has been reported that 0.1 m*M* $CeCl_3$ can alleviate the reduction in growth under adverse conditions was related to improving water status and photosynthesis in soybean seedlings (Mao *et al*., 2012). We speculate that 0.1 m*M* $CeCl_3$ alleviates the water stress and increases the photosynthesis might be associated with its effect on growth of plants in the present stress conditions. It has been reported that treatments with different Ce^{3+} affected the uptake of K, Mg, Ca, Na, Fe, Mn, Zn, Cu and Mo in the shoots and roots (Liu *et al*., 2012). Our results suggested that $CeCl_3$ treatment promoted the growth of *H. tuberosus* seedlings, which might be attributed to $CeCl_3$ application improving the uptake of mineral nutrition elements.

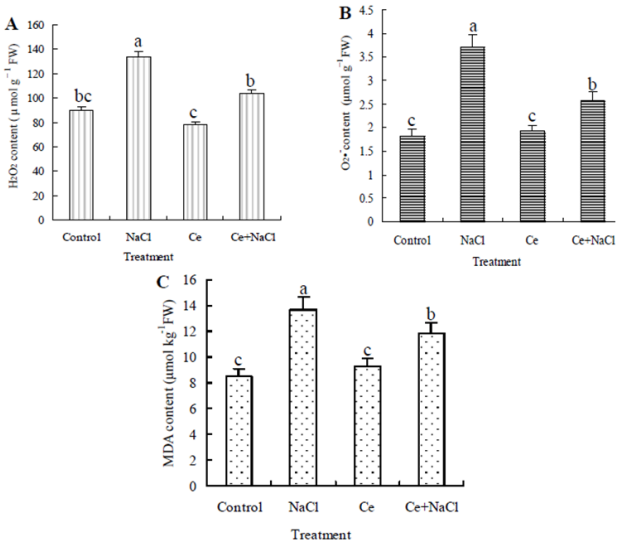

Fig. 1: Effect of $CeCl_3$ and NaCl on H_2O_2 (A), $O\cdot_2^-$ (B) and MDA (C) content in *H. tuberosus*. Each value represents the mean ± SD, n=3. Different letters within each graph indicate statistically significant differences at $P<0.05$ using Duncan's Multiple Range Test (DMRT)

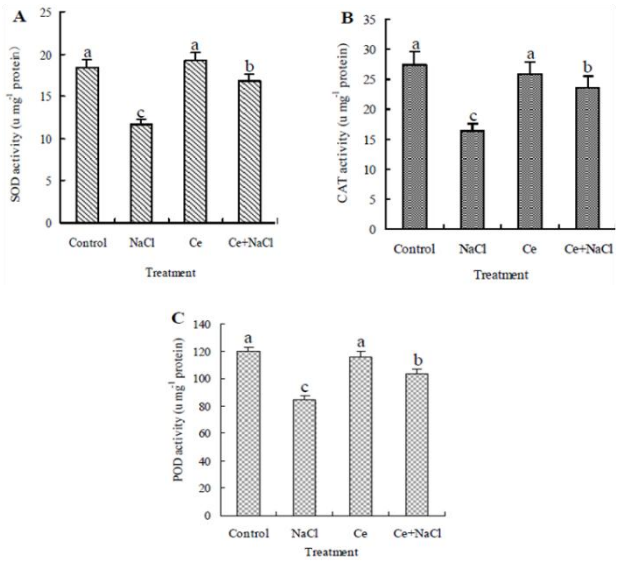

Fig. 2: Effect of $CeCl_3$ and NaCl on SOD (A), CAT (B) and POD (C) activities of *H. tuberosus.* Each value represents the mean ± SD, n=3. Different letters within each graph indicate statistically significant differences at $P<0.05$ using Duncan's Multiple Range Test (DMRT)

Chlorophyll content is an important index reflecting physiological state of leaf, corresponding well with photosynthetic capability (Xie *et al*., 2013). In green plants, oxidative stress is usually monitored by measuring chlorophyll content (MacFarlane, 2003; Liu *et al*., 2012). Our study showed that the content of chl-a, chl-b and total chlorophyll was significantly decreased when treatment with NaCl (150 m*M*), which was in consistent with the previous findings (Huang *et al*., 2012). It has been reported that the effect of Ce^{3+} on the chlorophyll contents was that Ce^{3+} increased the absorption of nitrogen and phosphorus (Liao *et al*., 1994; Hong *et al*., 2002; Song *et al*., 2003; Yin *et al*., 2009). In this study, the addition of 0.1 m*M* $CeCl_3$ could remarkably increase chl-a, chl-b and total chlorophyll contents in *H. tuberosus* seedling under salt stress or normal conditions. The most likely reason can be attributed to the absorption of nitrogen and phosphorus and subsequent induction of the synthesis of precursors of chlorophyll by $CeCl_3$.

It is clear that high salinity produces oxidative stress and increases reactive oxygen species (ROS) in plants, such as H_2O_2 and $O_2\cdot^-$ (Tanou *et al*., 2009). Overproduction of ROS might cause adverse effect that lead to extensive lipid peroxidation as indicated by higher accumulation of MDA in chloroplasts of plants (Gossett *et al*., 1994). In this study, high salinity significantly increases H_2O_2, $O_2\cdot^-$ and MDA content in *H. tuberosus* seedlings, implying that salt stress caused increased ROS production. Previous studies have found that REEs could protect plants against oxidative injury (Wang *et al*., 2011b; Xie *et al*., 2013). The reduction of Ce^{4+} to Ce^{3+} is thought to generate superoxide anions. It is postulated that Ce^{3+} can react with hydroxyl radicals and act as an antioxidant (Park *et al*., 2008; Celardo *et al*., 2011). In this experiment, 0.1 m*M* $CeCl_3$ decreased production of H_2O_2, $O_2\cdot^-$ and accumulation of MDA induced by salt stress, suggesting that $CeCl_3$ could directly remove ROS and protect plasma membrane lipid against oxidative damage.

In order to minimize oxidative damage in adverse environments plant cell has developed the antioxidant defense systems including antioxidative enzymes such as SOD, CAT and POD and antioxidant compounds (Mittler, 2002). SOD is the first line of defense which converts $O_2\cdot^-$ radicals into O_2 and H_2O_2. H_2O_2 is toxic and must be eliminated in subsequent reactions. In plant, CAT and POD played important roles to scavenge H_2O_2 from cells. CAT eliminates H_2O_2 by breaking it down directly to form O_2 and water. POD catalyzes H_2O_2-dependent oxidation of substrate (Zhao *et al*., 2008). In this paper, the activities of SOD, CAT and POD were significantly inhibited under salt stress, implying that exposure to high salinity resulted in an imbalance between ROS and their removal in *H. tuberosus* seedlings. Previous studies have shown that REEs could affect the activities of many antioxidative enzymes and antioxidant compounds in plants. It was reported that addition with $LaCl_3$ increased the activities of SOD, CAT, glutathione reductase (GR) and ascorbate peroxidase (APOX) in *Saussurea involucrata* under salt stress (Xu *et al*., 2008). Wang *et al*. (2011b) found that the treatments of $LaCl_3$, $CeCl_3$ and $NdCl_3$ significantly increased the activities of antioxidative enzyme in maize seedling under cold stress.

In this experiment, compared with NaCl treatment, addition of $CeCl_3$ could significantly increase the activities of SOD, CAT and POD in seedling exposed to salt stress implying that 0.1 mM $CeCl_3$ could increase the antioxidant defense abilities and alleviate the salt-induced oxidative damage of *H. tuberosus*.

Conclusion

Exogenous supply of 0.1 m*M* $CeCl_3$ could significantly promote the growth of *H. tuberosus*, increase leaf chlorophyll content, alleviate the oxidative damage and protect the antioxidant system from damage under salt stress. Further research should be strengthened for elucidating $CeCl_3$ induced changes at molecular and cellular level. Moreover, the safety of Ce^{3+} should be investigated in detail with in-depth studies on the effects of Ce^{3+} on cultivated *H. tuberosus*.

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