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BRIEF COMMUNICATION

Effects of lanthanum on the ascorbate and glutathione metabolism of *Vigna radiata* seedlings under salt stress

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Abstract

In order to elucidate the role of lanthanum (La) in response of *Vigna radiata* to a salt stress, we investigated the effects of La on the ascorbate and glutathione metabolism. The results show that in comparison with a control, the salt stress increased the activities of ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), γ-glutamylcysteine synthetase (γ-ECS), and L-galactono-1,4-lactone dehydrogenase (GalLDH), and the content of ascorbic acid (AsA) and glutathione (GSH). It also increased the malondialdehyde content (MDA) and electrolyte leakage. The salt stress significantly decreased the ratios of AsA/dehydroascorbate (DHA) and GSH/glutathione disulphide (GSSG) compared with the control. The pretreatment with La not only significantly increased the activities of the above enzymes, the content of AsA, GSH, and the ratios of AsA/DHA and GSH/GSSG, but also significantly reduced the MDA content and electrolyte leakage compared with the salt stress alone. Our results suggest that La could up-regulate the ascorbate and glutathione metabolisms and could have an important role for acquisition of salt stress tolerance in *Vigna radiata*.

Additional key words: ascorbate peroxidase, glutathione reductase, galactono-1,4-lactone dehydrogenase, γ-glutamylcysteine synthetase, mung bean, NaCl.

Salt stress is one of the main environmental factors that adversely affect plant growth, productivity and survival (Ellouzi *et al.* 2013). Salt stress usually induces the overproduction of reactive oxygen species (ROS) in plant cells (Ferreira-Silva *et al.* 2012, Ma *et al.* 2013). Plants can protect themselves against oxidative damage by enhancing their ROS-scavenging system including antioxidative enzymes and nonenzymatic compounds (Benzarti *et al.* 2012, Fatehi *et al.* 2012). Ascorbate and glutathione are two crucial nonenzymatic antioxidants. It is well known that plants can adjust ascorbate and glutathione content by modulating the regeneration and biosynthesis of ascorbate and glutathione. The L-galactose pathway is the main biosynthetic pathway of ascorbate in plants, and L-galactono-1,4-lactone dehydrogenase (GalLDH) is the last enzyme in this pathway (Wheeler *et al.* 1998). Further, γ-glutamylcysteine synthetase (γ-ECS) is the first enzyme for glutathione biosynthesis (Dringen 2000). The ascorbate-glutathione cycle is the recycling pathway for the regeneration of ascorbate and glutathione and so plays an important role in defence against oxidative damage induced by different stresses. In this cycle, ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) are the key enzymes.

It is well known that rare earth elements (REEs) form a special group and have interesting effects on plant

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Abbreviations: APX - ascorbate peroxidase; AsA - ascorbic acid; DHA - dehydroascorbate; DHAR - dehydroascorbate reductase; γ-ECS - γ-glutamylcysteine synthetase; GalLDH - L-galactono-1,4-lactone dehydrogenase; GR - glutathione reductase; GSH - reduced glutathione; GSSG - gluatahione disulphide; MDHAR - monodehydroascorbate reductase.

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growth (Ouyang *et al.* 2003). Lanthanum is an important rare earth element. Many studies show that the effects of La on plants depend on its concentration. In plants, it has been documented that a low concentration of La can promote root organogenesis (Guo *et al.* 2012), seed germination, and growth (Hong *et al.* 2003), mediates secondary metabolism (Zhou *et al.* 2012), regulates nitrogen assimilation (Huang *et al.* 2013), and replaces calcium in the process of stomatal closure (Xue and Yang 2005). However, the excess of La has negative effects on plants by inhibiting plant growth, destroying cell structure, and disturbing metabolism (Ruíz-Herrera *et al.* 2012, Liang and Wang 2013). Increasing evidence has proven that a low concentration of La can relieve oxidative damage in plants exposed to a variety of environmental stresses including salinity and drought (Zhang *et al.* 2006, Xu *et al.* 2007). However, little is known about the responses of the ascorbate and glutathione metabolisms in plants to La under salt stress. The aim of the study was to elucidate whether and how La regulates the activities of enzymes involved in ascorbate and glutathione metabolisms, the content of AsA and GSH, and the ratios of AsA/DHA and GSH/GSSG in leaves and roots of mung bean exposed to NaCl stress. The results can provide new knowledge for the possible application of La in agriculture.

Seeds of *Vigna radiata* (L.) Wilczek cv. Minglv245 were germinated in Petri dishes with filter paper moistened by distilled water in a climate chamber under a day/night temperatures of 25/15 °C, an air humidity of 65 %, an irradiance of 500 μmol m^{-2} s^{-1} (photosynthetically active radiation), and a 12-h photoperiod. When the first leaf was fully expanded, the seedlings were transferred into plastic boxes filled with a half-strength Hoagland's solution and kept their roots in dark. The nutrient solution was exchanged every two days. The seedlings (12-d-old) of uniform size were selected for experiments. After washing in distilled water for 12 h, the roots of seedlings were placed in beakers containing 100 cm^3 of a 120 mM NaCl solution at 25 °C for 24 h and at a continuous irradiance of 500 μmol m^{-2} s^{-1}. The beakers were wrapped with aluminium foil to keep roots in dark. In order to select a suitable concentration of La, we observe the wilting degree of the seedlings treated with NaCl + different concentrations of La (10, 30, 50, 70, and 90 μM). We found that 30 μM $LaCl_3$ could alleviate the most obviously the wilting symptoms. So, we used 30 μM $LaCl_3$ for further experiments. The plants were pretreated with 30 μM $LaCl_3$ for 12 h and then exposed to NaCl for 24 h under the same conditions as described above. The control plants were treated with distilled water. After the treatments, the samples of leaf and root were collected, frozen in liquid nitrogen, and then kept at -80 °C until used for analyses.

APX, GR, DHAR, and MDHAR were prepared by grounding each sample (0.5 g) into a fine powder in liquid nitrogen and then homogenizing the fine powder in 6 cm^3 of 50 mM KH_2PO_4 (pH 7.5) containing 0.1 mM ethylene-diaminetetraacetic acid, 0.3 % (v/v) *Triton X-100*, 1 % (m/v) polyvinylpolypyrrolidone, and 1 mM AsA for an APX assay (Grace and Logan 1996). The homogenate was centrifuged at 13 000 *g* and 2 °C for 15 min. The supernatant was used for assays. The activities of APX, GR, MDHAR, and DHAR were assayed according to Nakano and Asada (1981), Grace and Logan (1996), Miyake and Asada (1992), and Dalton *et al.* (1986), respectively.

GalLDH was prepared and measured by the method of Tabata *et al.* (2001) and γ-ECS was prepared and measured by the method of Rüeggseger and Brunold (1992). The content of AsA and DHA were measured according to Hodges *et al.* (1996). GSSG and GSH were measured according to Griffith (1980). A malondialdehyde content and electrolyte leakage were measured according to Hodges *et al.* (1999) and Zhao *et al.* (2004), respectively. A protein content was assayed according to Bradford (1976).

The experimental design was a complete random block design with five replications. Means were compared by the one-way analysis of variance (*ANOVA*) and the Duncan's multiple range test at the 5 % level of significance.

There were no obvious changes in the activities of APX, GR, DHAR, MDHAR, GalLDH, and γ-ECS in the leaves and roots of the control plants (Table 1). Compared with the controls, the salt stress significantly increased the activities of the above mentioned enzymes at 12 and 24 h of the treatment, and the pretreatment with La further increased these activities. After 24 h of the treatment, the activities of APX, GR, DHAR, MDHAR, GalLDH, and γ-ECS in the pretreated leaves increased by 24.0, 26.9, 45.4, 70.0, 53.3, and 35.3 %, respectively, compared to those only NaCl treated.In the roots, the activities increased by 62.8, 82.3, 30.8, 30.0, 38.5, and 44.4 %, respectively (Table 1).

The salt stress significantly increased the content of AsA, total ascorbate, GSH, and total glutathione at 12 and 24 h of the NaCl treatment compared with the control. The pretreatment with La further increased the content of AsA, GSH, and total glutathione (Table 1). Due to the La pretreatment, the content of AsA, GSH, total ascorbate, and total glutathione in the leaves and roots increased after 24 h of the NaCl treatment by 37.7, 36.6, 21.3, and 28.2 %, respectively, and by 17.0, 34.3, 11.1, and 24.4 %, respectively.

The salt stress decreased the ratios of AsA/DHA and GSH/GSSG in the leaves and roots at 12 and 24 h of the treatment compared with the control. The pretreatment with La significantly increased these ratios in the stressed leaves and roots compared with the salt stress treatment (Table 1). After 24 h of the NaCl treatment, the ratios of AsA/DHA and GSH/GSSG in the leaves increased by 51.8 and 95.0 %, respectively, and in the roots by 61.4 and 108.3 %, respectively.

Table 1. The effects of La on the activities of enzymes involved in the ascorbate and glutathione metabolism, on the ratios of AsA/DHA and GSH/GSSG, on malondialdehyde content, and on electrolyte leakage in leaves and roots of *Vigna radiata* under a salt stress. The plants were treated as follows: Control - distilled water; NaCl - 120 mM NaCl for 12 or 24 h; $LaCl_3$ + NaCl, a pretreatment with 30 μM $LaCl_3$ for 12 h + a treatment with 120 mM NaCl for 12 or 24 h. Means ± SE, $n = 5$. Different letters within the same row indicate statistically significant differences according to Duncan's test ($P < 0.05$). One unit of APX was defined as the amount of APX catalyzing the oxidation of 1 μmol of ascorbate per minute. One unit of GR activity was defined as the reduction of 1 μmol of NADPH per minute. One unit of DHAR activity was defined as the amount of enzyme that produces 1 μmol of AsA per minute. One unit of MDHAR activity was defined as the amount of enzyme that oxidizes 1 μmol of NADH per minute. One unit of GalLDH activity was defined as the amount of extract required to oxidize 1 nmol of *L*-Gal (equivalent to the formation of 2 nmol of reduced Cyt *c*) per minute. One unit of γ-ECS activity was defined as 1 μmol of cysteine-dependently generated PO_4^{3-} per minute.

Parameters	Time [h]	Control roots	Control leaves	NaCl roots	NaCl leaves	$LaCl_3$ + NaCl roots	$LaCl_3$ + NaCl leaves
APX [U mg^{-1}(protein)]	12	1.11±0.10c	1.45±0.11c	1.98±0.18b	2.26±0.14b	2.52±0.17a	3.00±0.20a
	24	1.20±0.11c	1.40±0.09c	1.75±0.16b	2.50±0.16b	2.85±019a	3.10±0.22a
GR [U mg^{-1}(protein)]	12	1.30±0.09c	1.50±0.12c	1.85±0.13b	2.40±0.16b	2.71±0.21a	3.40±0.22a
	24	1.10±0.10c	1.62±0.12c	1.70±0.11b	2.60±0.18b	3.10±0.20a	3.30±0.21a
DHAR [U mg^{-1}(protein)]	12	0.30±0.02c	0.60±0.03c	1.50±0.13b	1.20±0.08b	2.00±0.18a	1.80±0.16a
	24	0.40±0.02c	0.50±0.03c	1.30±0.11b	1.10±0.07b	1.70±0.15a	1.60±0.12a
MDHAR [U mg^{-1}(protein)]	12	0.60±0.03c	0.40±0.02c	1.20±0.11b	1.00±0.07b	1.60±0.13a	1.50±0.11a
	24	0.50±0.03c	0.50±0.03c	1.00±0.07b	1.00±0.06b	1.30±0.12a	1.70±0.15a
γ-ECS [nmol mg^{-1}(protein) min^{-1}]	12	0.60±0.03c	1.00±0.09c	1.00±0.08b	1.50±0.12b	1.50±0.11a	2.00±0.17a
	24	0.60±0.03c	1.10±0.09c	0.90±0.08b	1.70±0.13b	1.30±0.12a	2.30±0.15a
GalLDH [U g^{-1}(f.m.)]	12	0.70±0.05c	1.00±0.07c	1.20±0.10b	1.50±0.13b	1.80±0.15a	2.20±0.15a
	24	0.90±0.07c	0.80±0.05c	1.30±0.11b	1.50±0.11b	1.80±0.16a	2.30±0.16a
AsA content[μmol g^{-1}(f.m.)]	12	4.30±0.28c	5.10±0.35c	4.90±0.31b	6.30±0.46b	5.80±0.38a	7.90±0.55a
	24	4.00±0.24c	5.00±0.31c	4.70±0.31b	6.10±0.42b	5.50±0.35a	8.40±0.63a
Total ascorbate [μmol g^{-1}(f.m.)]	12	4.50±0.26c	5.30±0.33c	5.60±0.36b	7.00±0.52b	6.30±0.47a	8.49±0.65a
	24	4.20±0.24c	5.20±0.34c	5.40±0.33b	6.80±0.47b	6.00±0.43a	9.10±0.77a
GSH content [μmol g^{-1}(f.m.)]	12	0.25±0.01c	0.31±0.02c	0.33±0.02b	0.43±0.03b	0.43±0.03a	0.55±0.04a
	24	0.28±0.01c	0.29±0.01c	0.35±0.02b	0.41±0.03b	0.47±0.03a	0.56±0.04a
Total glutathione [μmol g^{-1}(f.m.)]	12	0.26±0.01c	0.33±0.02c	0.38±0.03b	0.49±0.03b	0.46±0.03a	0.59±0.04a
	24	0.29±0.02c	0.30±0.02c	0.41±0.03b	0.46±0.03b	0.51±0.03a	0.59±0.03a
AsA/DHA	12	25.00±1.70a	24.00±1.65a	7.50±0.45c	9.00±0.64c	12.20±1.00b	13.30±1.10b
	24	25.00±1.79a	24.50±1.58a	7.00±0.50c	8.10±0.51c	11.30±0.96b	12.30±1.03b
GSH/GSSG	12	23.00±1.56a	19.00±1.33a	6.60±0.50c	7.00±0.51c	14.00±1.00b	12.30±0.86b
	24	21.00±1.33a	24.00±1.53a	6.00±0.45c	8.00±0.66c	12.50±1.20b	15.70±1.11b
MDA content [nmol g^{-1}(f.m.)]	24	7.50±0.63c	5.00±0.35c	17.00±1.40a	13.00±1.01a	13.00±1.10b	9.00±0.77b
Electrolyte leakage [%]	24	12.00±1.10c	10.00±0.85c	30.00±1.52a	25.00±1.21a	20.00±1.50b	17.00±1.30b

The salt stress significantly increased the electrolyte leakage and the malondialdehyde content in the leaves and roots,compared to the control. The pretreatment with La significantly decreased the electrolyte leakage and the malondialdehyde content, compared to the salt stress (Table 1). These results suggest that the pretreatment with La had an important role for acquisition of salt stress tolerance in *V. radiata*.

The cellular content of ascorbate can be controlled by APX, DHAR, MDHAR, and GalLDH. It has been reported that La can increase APX activity in *Saussurea involucrata* under salt stress (Xu *et al.* 2007). In the present study, we also found that La increased the APX activity in the leaf and root of *V. radiata* under the salt stress. Besides, we also found that La increased the contents of AsA and total ascorbate, and the ratio of AsA/DHA in the leaves and roots of *V. radiata* under the salt stress by increasing the activities of DHAR, MDHAR, and GalLDH. Glutathione is another important compound in the plant antioxidant system. The content of GSH can be determined by activities of γ-ECS and GR. It has been reported that La could increase GR activity in *Saussurea involucrata* under salt stress (Xu *et al.* 2007). In present study, we also found that La increased GR activity in leaf and root of *V. radiata* under salt stress. Besides, we also found that La regulated the contents of GSH and total glutathione, and the GSH/GSSG by increasing γ-ECS activity.

The root system is the first part of the plant affected by excess of NaCl, and the biochemical responses of roots are important for adaptation. It has been documented that salt stress can increase the activities of

antioxidant enzymes in roots of many plants, which, protected the roots of plants against the oxidative stress (Bandeoğlu *et al.*, 2004, Rubio *et al.* 2009). In the present study, we found that NaCl stress increased the activities of enzymes involved in the metabolism of ascorbate and glutathione and so protect the roots. It has been reported that La could promote root growth at low concentrations, but cause damage to roots at high concentrations (Ruíz-Herrera *et al.* 2012). Increasing evidences also showed that low concentration of La could protect plants against abiotic stresses (Xu *et al.* 2007, Zhang *et al.* 2006). In our study, we also found that low concentration of La could protect roots against the salt stress, which, in turn, alleviated the wilting degree of plants.

Jasmonic acid (JA) plays important role in regulating stress responses, plant growth, and development (Bandurska *et al.* 2003, Sasaki-Sekimoto *et al.* 2005). The content of jasmonates increases during stresses and they can improve antioxidative ability of plants under stress conditions (Bandurska *et al.* 2003). In our previous study, we showed that JA could regulate the ascorbate-glutathione cycle under water stress (Shan and Liang 2010). Zhou *et al* (2012) reported that JA mediated the secondary metabolism regulated by La. However, it is not known whether JA is involved in the responses of the ascorbate and glutathione metabolism to La under salt stress. Therefore, the role of JA in the responses of the ascorbate-glutathione cycle to La under salt stress will be investigated in our future research.

The presented results indicate that La enhanced the antioxidant ability and protects *V. radiata* against NaCl stress by participating in the regulation of ascorbate and glutathione metabolism. Therefore, La can be used in agriculture to improve the salt tolerance of *V. radiata*.

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