

Analysis of the combined effects of lanthanum and acid rain, and their mechanisms, on nitrate reductase transcription in plants

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ABSTRACT

Rare earth element (REE) pollution and acid rain are major global environmental concerns, and their spatial distributions overlap. Thus, both forms of pollution combine to act on plants. Nitrogen is important for plant growth, and nitrate reductase (NR) is a key plant enzyme that catalyzes nitrogen assimilation. Studying the combined effects of REEs and acid rain on plant nitrogen-based nutrients has important environmental significance. Here, soybean (*Glycine max*) plants, commonly used for toxicological studies, were exposed to lanthanum (La), a REE, and acid rain to study the NR activities and NR transcriptional levels in the roots. To explain how the pollution affected the NR transcriptional level, we simultaneously observed the contents of intracellular La and nutrient elements, protoplast morphology, membrane lipid peroxidation and intracellular pH. A combined treatment of 0.08 mmol/L La and pH 4.5 acid rain increased the NR activity, decreased the NR transcriptional level, increased the intracellular nutrient elements' contents and caused deformations in membrane structures. Other combined treatments significantly decreased the aforementioned parameters and caused serious damage to the membrane structures. The variation in the amplitudes of combined treatments was greater than those of individual treatments. Compared with the control and individual treatments, combined treatments increased membrane permeability, the malondialdehyde content, and intracellular H⁺ and La contents, and with an increasing La concentration or acid strength, the change in amplitude increased. Thus, the combined effects on NR gene transcription in soybean seedling roots were related to the intracellular nutrient elements' contents, protoplast morphology, membranous lipid peroxidation, intracellular pH and La content.

1. Introduction

Rare earth elements (REEs) are widely used in industry, agriculture, medicine, environmental protection, and other areas because of their physical and chemical properties, resulting in the increase in their contents in the environment (Hu et al., 2006; Redling, 2006), and affecting plant growth (D'Aquino et al., 2009; Liu et al., 2012). For example, in China, the average content of REEs in soil and river sediments has been up to 176.8 µg/g and 229.7 µg/g, respectively (Zhou et al., 2012; Liang et al., 2014a, 2014b). The average content of REEs in the global soil has been up to 193.8 µg/g. In China (Beijing), Japan (Osaka) and Germany (Delft), the average content of REEs in the atmosphere is 94.65, 23.39 and 4.35 ng/m³, respectively (Liang et al., 2014a, 2014b). Acid rain is a major global environmental problem

(Rodhe et al., 2002; Wai et al., 2005), and China is the third largest country polluted by acid rain in the world, after Europe and North America (Larsen et al., 2006), and the average pH value of acid rain in China ranges from 3.0 to 4.5 (Department EoCE, 2015; Wang et al., 2016a, 2016b). When the intensity of acid rain reaches a certain harmful threshold, it can affect plant growth through direct acute damage and indirect acidified soil (Singh and Agrawal, 2008; Shukla et al., 2013). Because a great number of agro-ecological systems are in acid rain-prone areas, they overlap with areas having other contaminants, such as REEs (Wei et al., 2001), leading to combined effects of REEs and acid rain on plants in the same space and time. Thus, the combined REE and acid rain pollution is a problem that influences environmental safety and requires scientific examination.

The non-moving property of terrestrial plants exposes them to the

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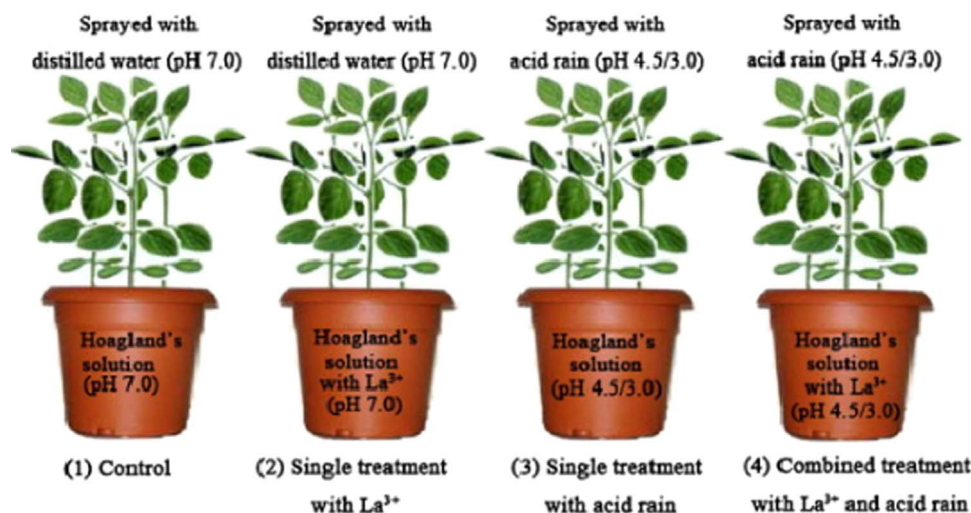


Fig. 1. Schematic of different treatments.

combined pollution of REEs and acid rain. This combined pollution has harmful effects on plant growth, and the effects are related to the inhibition of plant photosynthesis and the decrease in assimilate synthesis (Wen et al., 2011). However, plant growth is not only affected by the photosynthesis of plant organs above ground, but is also affected by the mineral nutrition absorbed by its underground roots. For example, nitrogen absorbed by plant roots is converted to organic nitrogen compounds through nitrate (NO_3^-) and ammonium assimilation. Then, it enters the amino acid metabolism (Buchanan et al., 2000), meeting the demand of plant cell growth and proliferation for amino acids and proteins, and ultimately it affects the normal growth and development of the whole plant (Buchanan et al., 2000). The plant nitrogen pathway is important in studying the effects of typical environmental pollution on plant life (Balestrasse et al., 2003; Song et al., 2003). Previous studies found that the growth of soybean seedling roots under the combined treatment of lanthanum (La), a REE, plus acid rain was related to the nitrogen level (Sun et al., 2013). It has been reported that nitrate reductase (NR) is the primary rate-limiting enzyme of nitrogen nutrition (Campbell, 1999; Solomonson and Spehar, 1977). The regulation of adverse conditions on NR protein synthesis occurs mainly at the transcriptional level (gene expression) (Deng et al., 1990; Crawford, 1995). The intracellular nutrient elements are important limiting factors to influence the transcription and synthesis of NR (Buchanan et al., 2000; Kaiser and Huber, 2001), and their contents are related to the structure and integrity of the plasma membrane (Buchanan et al., 2000; Campbell, 1999). The resulting problems are: (1) Whether rare earth La and acid rain have a combined effect on NR transcription? and (2) What are the reasons for the combined effects of rare earth La and acid rain on the NR transcription? The answers to the above questions will help to elucidate the mechanism of the combined effects of La and acid rain on nitrogen nutrition in plant roots.

Here, we selected soybean (*Glycine max*, 'Huang 25') as the experimental material because it is commonly used in toxicological studies and is recommended by the United States Environmental Protection Agency (Raney, 2006). We studied the combined effects of La and acid rain on NR activity and the NR transcriptional level in soybean seedling roots, and examined cell membrane morphology, intracellular elements, intracellular pH and membrane lipid peroxidation in soybean roots. Then, we discussed the combined effects of La and acid rain on NR in soybean seedling roots at the cellular and molecular levels. The aim was to analyze how the combined pollution changed the activity and transcriptional levels of NR, and nitrogen nutrition in soybean seedling roots.

2. Materials and methods

2.1. Plant materials and experimental designs

Soybean seedlings were cultured as described in our previous study (Sun et al., 2011; Wen et al., 2011). Sterilized seeds of soybean ('Zhonghuang 25'; Wuxi Seed Co., Ltd., China) were germinated and grown at $25 \pm 5^\circ\text{C}$, $300 \mu\text{mol}/(\text{m}^2 \text{ s})$ light intensity, and 16/8 h day/night cycles in a greenhouse. Fifteen-day-old seedlings were cultured in half-strength Hoagland's solution. The air supply during hydroponic cultivation was provided by an aquarium air pump in the medium solution. The nutrient solution was renewed every 3 d to stabilize its pH value. Then, 25-day-old seedlings of similar size were selected for the experiments. The La solutions (0.08, 0.40, and 1.20 mM) (Pang et al., 2002; Wen et al., 2011), acid rain solutions (pH 3.0 and 4.5) (Li et al., 2010), and mixed solutions of La and acid rain were prepared according to previously reported methods (Wen et al., 2011). The acid rain stock solution at pH 1.0 was prepared with a solution of concentrated sulfuric acid and nitric acid at a 3:1 ratio (v/v, by chemical equivalents), according to the general anion composition of rainfall in China (2007–2008) (Chen et al., 2010). Given the extremely low solubility of the REE phosphate, 1 mM KH_2PO_4 in the Hoagland's solution (pH 7.0) was replaced by 1 mM KCl to avoid phosphate precipitation. This solution was called the -P nutrient solution. The seedlings were subjected to 12 treatments, as shown in Fig. 1. First, the control treatment, in which soybean seedlings were cultured in the -P nutrient solution (pH 7.0) and sprayed with distilled water until drops began to fall from the leaves. Second, the La treatment, in which soybean seedlings were cultured in the -P nutrient solution with La (0.08, 0.40, and 1.20 mM at pH 7.0), and then sprayed with distilled water until drops began to fall. Third, the acid rain treatment, in which soybean seedlings were cultured in the acidic -P nutrient solution (pH 3.0/4.5) and sprayed with acid rain at the same pH on the foliage until drops began to fall. Fourth was the combined treatment of La and acid rain. Soybean seedlings were cultured in the acidic -P nutrient solution with La (0.08, 0.40, and 1.20 mM at pH 3.0/4.5), and then sprayed with acid rain at the same pH until drops began to fall. All of the treatments were performed in five replicates, and 1 mM KH_2PO_4 was sprayed on the foliage every other day to supply the required inorganic phosphate. After 7 d of the La and acid rain treatments, the roots were collected for the determination of the test indices.

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