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Effects of silicon on absorbed light allocation, antioxidant enzymes and ultrastructure of chloroplasts in tomato leaves under simulated drought stress

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ABSTRACT

The impact of silicon (Si) on chlorophyll fluorescence, antioxidant enzymes and the ultrastructure of chloroplasts of drought-stressed tomato (*Solanum lycopersicum* L.) was investigated. Si reduced the accumulation of reactive oxygen species (ROS) and malondialdehyde (MDA) in chloroplasts. Si-induced improvement of absorbed light allocation in leaves reduced the risk of ROS generation. Drought stress increased the relative deviation from full balance between the two photosystems ($\beta/\alpha - 1$) and PSII excitation pressure (1 – qP). Application of Si restrained chlorophyll degradation and increased optimal photosynthetic efficiency of PSII (Fv/Fm) and the electron transport rate (ETR), which contributed to improvement of the net photosynthetic rate (Pn), ($\beta/\alpha - 1$) and (1 – qP). On the other hand, Si-mediated enzymatic systems contributed to ROS elimination. The dual nature of ROS was detected during 12 days of drought stress. While Si played an important role in suppressing the decline of the activities of ROS scavenging enzymes in chloroplast, such as superoxidase dismutase (SOD) and enzymes in the ascorbate–glutathione pathway. Therefore, Si protected the structure of the chloroplast from severe oxidative damage, such as the distortion of the grana lamellae and stroma lamellae. This study suggested that Si might be involved in metabolic or physiological activities in Si non-accumulating plants under drought stress.

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1. Introduction

Numerous physiological, metabolic and morphological changes are common in plants subjected to drought stress (Hasanuzzaman et al., 2014). Si may be a 'quasi-essential' element for plants and the beneficial effects of Si on plant, from biotic and abiotic stresses, have been increasingly recognized (Pilon-Smits et al., 2009). Supplementation with Si has been adopted as an effective strategy for alleviating the negative effects of drought stress and improving the drought resistance of plants (Zhu and Gong, 2014).

Previous investigations have documented the effects of Si on photosynthesis and chlorophyll fluorescence of plants under drought stress. In contrast with the non-Si treatment, application of Si under drought stress increased photosynthesis of rice (*Oryza sativa* L.) (Chen et al., 2011) and the net CO_2 assimilation rate of wheat (*Triticum aestivum* L.) (Gong et al., 2005). Generally, Si-mediated improvement in photosynthesis under drought stress is associated with increases in photosynthetic pigments and activities of certain photosynthetic enzymes (Gong and Chen, 2012; Pei et al., 2010). Moreover, primary reactions of photosynthesis are reflected in chlorophyll fluorescence, which has been used widely to assess the plant response to environmental stress (Sayed, 2003). Si is engaged in suppressing salinity-induced increase in non-photochemical quenching (NPQ) (Mateos-Naranjo et al., 2013) and drought-induced decrease in (Fv/Fm) (Chen et al., 2011). As we all know, incomplete consumption of absorbed light energy is apt to increase transfer of excess excitation energy to oxygen, which accelerates the overproduction of reactive oxygen species (ROS) (Golding and Johnson, 2003). Therefore, the development of mechanisms for dissipating or avoiding the production of such excess energy can affect acclimation to drought-induced oxidative stress in cells. However, information is scarce on the role of Si in balancing excess excitation energy in plants under drought stress.

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In addition, Si-mediated antioxidant defense can alleviate oxidative damage in drought-stressed plants. Si partially counters the negative effects of drought on plants by regulating the oxidative damage antioxidase enzyme system. Catalase (CAT, EC 1.11.1.6), (POD, EC 1.11.1.7) and enzymes in the ascorbate–glutathione cycle can detoxify H_2O_2, to which superoxide anion ($O_2^{\bullet -}$) is dismutated by SOD (EC 1. 15.1.1). Si increases the activities of SOD, CAT, and glutathione reductase (GR) of wheat (*T. aestivum* L.) under drought stress and decreases hydrogen peroxide (H_2O_2) content and oxidative damage (Pei et al., 2010). Whereas, the effects of Si on enzyme activities vary among cultivars. Shen et al. (2010) confirmed that Si decreased the activity of SOD, peroxidase POD and CAT. In addition, the ability of Si to offset drought-induced oxidative damage may be related to stress intensity (Gong et al., 2008). Although many studies on Si-mediated cellular defense responses to drought-induced oxidative stress have been done, few of them focus on effects of Si on subcelluar ROS-scavenging enzymes under drought stress.

Tomato (*Solanum lycopersicum* L.) is grown worldwide and is regarded as a non-accumulator of Si, having displayed passive absorption of Si (Mitani and Ma, 2005). Whereas Si was shown to contribute to the yield of cherry tomato (Toresano-Sánchez et al., 2012). Our previous study addressed that Si can promote the growth and photosynthesis of tomato (Cao et al., 2013). The effects of Si on salt-stressed tomatoes have also been investigated extensively (Zhu and Gong, 2014). These observations may be consistent with Katz (2014), who suggested the regulation of Si on low Si-accumulating plants is not insignificant.

To our knowledge, investigations on Si-mediated alleviation of drought stress in plants have largely been restricted to high-Si-accumulating monocotyledons. Studies on Si non-accumulating dicots are relatively few in number. Furthermore, current studies provide little direct evidence of the impact of Si on drought-induced oxidative stress in tomato cell organelles. Absorbed light allocation and antioxidant enzymes at the subcellular level have not been considered simultaneously. In this study, we investigated absorbed light allocation, chloroplast ultrastructure and the activities of several important enzymes involved in the antioxidant system of chloroplasts in tomato mesophyll cells under drought stress. The objective was to give a systematic view on the role of Si in balancing ROS production in photosynthetic tissues and ROS removal at the organelle level, expounding regulatory mechanisms of Si in Si non-accumulating plants grown under drought stress.

2. Materials and methods

2.1. Growth conditions and experimental design

After being soaked in Si-deprived water provided by “qian jing” Environmental Protection Equipment Co., in Canton, tomato seeds were germinated between two layers of gauze that absorbed Si-deprived water. The germinated seeds were sown in a hydroponic device that used loose floss silk as a growth medium. After emergence of the first true leaf, the seedlings were transplanted to crystal plastic-lined plastic pots, with one plant per pot and 1.5 L of complete nutrient Hoagland solution aerated using an air pump. When the plants grew to a biomass of 9 true leaves, uniformly-growing ones of tomato seedings were taken for experimental treatment. Experimental treatment time was 12 days, during which tomato seedings were sampled for analysis of relevant parameters.

Our previous experiments showed that Si is beneficial to photosynthesis of tomatoes grown under normal conditions (Cao et al., 2013). Two sets of experiments were carried out in the current study. In the first set, multi-Si level tests were designed to select the optimum doses of Si for mitigation of simulated drought stress imposed by (w/v) 1% polyethylene glycol 6000 (PEG). The five treatments were: (a) full Hoagland nutrient solution; (b) PEG, full Hoagland nutrient solution plus 1% PEG; (c) PEG + Si0.6, full Hoagland nutrient solution plus 1% PEG and 0.6 mM Si; (d) PEG + Si1.2, full Hoagland nutrient solution plus 1% PEG and 1.2 mM Si; (e) PEG + Si1.8, full Hoagland nutrient solution plus 1% PEG and 1.8 mM Si. In the second set of experiment, following emergence of two true leaves, the seedlings were divided randomly into three groups. One group was pre-cultured under 0.6 mM Si prepared with Na_2SiO_3, and the other two groups were cultured with full nutrient solution. Until plants had four true leaves, the three treatments were: (f) CK, full nutrient solution; (j) PEG, full nutrient solution plus 1% PEG; (h) PEG + Si, full nutrient solution plus 1% PEG and the optimum dose of Si obtained from the first set of experiments.

Because it can be altered by the addition of Si, the osmotic potential was balanced by adding Na_2SO_4 to the CK and PEG treatments. The pH of nutrient solutions was adjusted to 6.0 and they were renewed every 2 days and were continuously aerated. Plants were grown in the greenhouse under natural light at an intensity of 1400–1800 $\mu mol\ m^{-2}\ s^{-1}$ (midday of a sunny day), temperatures of 28–32 °C/18–21 °C (day/night), and relative humidities of 67–92%. After 12 days of PEG-simulated drought, the third fully expanded mature leaf, numbered basipetally, was subjected to measurement of electrolyte leakage, net photosynthetic rate (Pn), chlorophyll fluorescence, chlorophyll analysis, antioxidant enzyme activities and visualization of chloroplast ultrastructure.

2.2. Electrolyte leakage

Electrolyte leakage was measured according to Bajji et al. (2002), with a slight modification. Fifteen fresh leaf discs (1.2-cm diameter) rinsed with demineralized water were placed in an airproof tube containing 25 mL of demineralized water, and subsequently were vacuumed for 20 min. The initial conductivity value of the solution was determined after 4 h at room temperature, using a conductivity meter. The tube was placed in a boiling water bath for 10 min and cooled to room temperature. Total conductivity was recorded after 20 min. Initial conductivity was expressed as a percentage of total conductivity.

2.3. Biomass and silicon concentration of plants

After 12 days of PEG-simulated drought, the treated tomato plants were sampled to measure plant biomass and silicon content. For plant biomass, shoots and roots were respectively weighed, after the measurement of plant height and stem diameter. Roots, stems, leaves were dried at 75 °C and grounded into powders. 0.3 g of tomato roots, stems, leaves powders were ashed in crucibles for 3 h at 300 °C, and then for 4 h at 550 °C. The ash was dissolved in a mixed solution of 50 mL 0.08 mol L^{-1} H_2SO_4 and 40% HF (hydrogen fluoride) 2 mL, then the Si concentrations in the mixed solutions were measured by the colorimetric molybdenum blue method at 811 nm (Van, 1987) with a spectrophotometer (SHIMADZU UV-2450, Japan).

2.4. Net photosynthetic rate (Pn), chlorophyll analysis and chlorophyll fluorescence parameters

The net photosynthetic rate (Pn) was measured on the leaves of three plants for each treatment using a CIRAS-1 Portable Photosynthesis System CIRAS-1 (PPsystems, Hitchin, Herdfordshire, UK), at 10:00–11:00 am. Chlorophyll was extracted from ten 1.2-cm-diameter leaf discs per functional leaf by submerging the discs in 20 mL of a mixture of absolute alcohol and acetone (5:5 v/v) in the dark until the discs were completely void of color. Chlorophyll was quantified following the method of Inskeep and Bloom (1985).

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