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ORIGINAL PAPER

Silicon effects on antioxidative enzymes and lipid peroxidation in leaves and roots of peanut under aluminum stress

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Abstract Silicon (Si) can enhance plant defense against biotic and abiotic stresses, but little is known of its possible alleviation of aluminum (Al) stress. In this study, we find out how Si may mediate Al stress based on changes in root morphological parameters, biomass, physiological attributes and concentrations of Al and Si in peanut (*Arachis hypogaea* L., cv. Zhongkaihua 99). The peanut was raised with (80 mg L^{-1}) or without Si in the growth chamber under 0 and toxic Al (160 mg L^{-1}) levels. Aluminum stress reduced the root dry weight by 52.4 %, shoot dry weight by 33.9 % and root-to-shoot ratio (R/S) by 28.8 %. However, it increased the activities of catalase in leaves and roots by as much as 161.6 and 149.0 %, superoxide dismutase by 141.7 and 147.0 %, and peroxidases by 62.0 and 64.1 %. The Si-treated peanut suffered less from Al stress through improvements in photosynthesis, biomass and R/S. The malondialdehyde, an index of membrane damage decreased significantly by 26.0 and 28.2 % in peanut leaf and root with silicon application under Al toxicity. For the peanut treated with Al, tissue concentration of Al increased by 371.5 % in the root, 20.9 % in the stem and 37.8 % in the leaf, much of the uptake was partitioned to the root. These concentrations decreased by 40.7, 5.3 and 25.6 %, respectively, following Si application.

Keywords Peanut · Silicon · Aluminum stress · Antioxidative enzymes · Lipid peroxidation

Introduction

Aluminum (Al) toxicity is a serious factor limiting crop productivity in acid soil, widely distributed in tropical and subtropical regions. The most easily recognized symptom of A1 toxicity is the inhibition of root growth, which can begin to inhibit root growth within 60 min (Ryan et al. 1993). When the concentration is greater than 2–3 ppm with a soil pH <5.5, Al solubility increases rapidly and affects root system, plant growth and yield (Balsberg-Pahlsson 1990; Zheng et al. 2005; Zhang et al. 2007).

The production of reactive oxygen species (ROS) under Al stress condition has been also demonstrated with different plant (Ryan et al. 1993; Wang et al. 2004; Kovacik et al. 2008; Du et al. 2010). Such species include singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet-}$), hydroxyl radicals (OH·) and toxic hydrogen peroxide (H_2O_2) molecules. Plants have developed a wide range of non-enzymatic and enzymatic defense mechanisms to scavenge the free radicals to avoid or limit destructive oxidative stress (Parida et al. 2004; Kovacik et al. 2008; Triantaphylides and Havaux 2009; Gill and Tuteja 2010). The antioxidant defense system includes non-enzymatic antioxidants such as glutathione (GSH), ascorbic acid (AsA), α-tocopherol, proline and carotenoids, whereas antioxidant enzymes also include superoxide dismutase (SOD, EC 1.15.1.1), catalase (CAT, EC 1.11.1.6) and peroxidases (POD, EC 1.11.1.7) (Farooq et al. 2013). Superoxide dismutase is a scavenger enzyme which catalyses the toxic $O_2^{\bullet-}$ radicals and results in the formation of H_2O_2 that is subsequently converted to H_2O by enzyme peroxidase (Triantaphylides and Havaux

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2009). The production of H_2O_2 is broken down into water and molecular oxygen by POD and CAT (Sairam and Srivastava 2001; Du et al. 2010). So, the antioxidant systems play important roles in protecting plants from oxidative damage (Shi et al. 2005).

Silicon (Si) is not considered an essential nutrient for higher plants, but it is typically abundant in soils (Epstein 1999). Its beneficial effects on plant growth have been widely evidenced, especially for plants subjected to biotic and abiotic stresses, such as diseases, pests, drought, salinity, cold, heavy metals, UV-B radiation and nutrient imbalance (Epstein 1999; Ma 2004; Eneji et al. 2005; Liang et al. 2007; Kaya et al. 2009; Shen et al. 2009, 2010a, b). Silicon-mediated Al toxicity has been reported in several plant species, such as tomato (Peaslee and Frink 1969), sorghum (Hodson and Sangster 1993), barley (Hammond et al. 1995), wheat (Cocker et al. 1998) and maize (Kidd et al. 2001; Wang et al. 2004).

However, there is little information on the possible use of Si for improving Al-toxicity tolerance in peanut or any plant of the leguminosae family. A hydroponic experiment was conducted to determine the effect of Si application on growth, antioxidant enzymes, and Al and Si uptake in peanut seedlings under Al stress. The objective was to investigate whether or not the application of Si activates the protective responses in peanut plants exposed to Al stress.

Materials and methods

Plant material and growth conditions

This experiment was conducted in Weed Research Laboratory of College of Agriculture in South China Agricultural University, Guangzhou, China. Peanut (*Arachis hypogaea* L., cv. Zhongkaihua 99) was purchased from Zhongkai University of Agriculture and Engineering, which is a small Spanish type peanut grown widely in South China. Seeds were first sterilized with 0.5 % NaOCl solution for 10 min, and then germinated in plastic boxes (20 × 30 × 10 cm) in the dark for 4 days in a growth chamber. After germination, the uniform seedlings were transferred to 12 pots (40 × 30 × 20 cm), each filled with half-strength Hoagland's nutrient solution and cultured as described in Shen et al. (2010a, b), with 8 seedlings per pot. Full strength solution was changed after 3 days, and Si was applied at 80 mg L^{-1} sodium metasilicate ($Na_2SiO_3{\cdot}9H_2O$), control without Si.

The seedlings were then exposed to 160 mg L^{-1} Al^{3+} ($AlCl_3{\cdot}6H_2O$) (pH 5.0) control solution without Al. This experiment was designed with four replications. 7 days after seedlings exposed to Al stress, it was sampled for the following tests.

Root morphological parameters and dry mass

Root surface area (RSA) and average root diameter (RD) were measured using the WinRHIZO image analysis system (WIN MAC, Regent Instruments Inc., Quebec, Canada). Plant was sampled and cut into shoots and roots, and then oven-dried (70 °C) and their dried mass is determined.

Gas exchange measurement

Gas exchange was measured 7 days after treatments. The net photosynthesis rates (P_N), stomatal conductance (Sc), transpiration rates (Tr), and internal CO_2 concentration (Ci) were measured using a portable infrared gas analyzer (LI-6400, Li-Cor Inc., Lincoln, NE, USA). Measurements were carried out at 25 °C.

Assays of antioxidant enzyme

Leaves and roots of peanut were homogenized using a mortar and pestle in a medium containing 50 mM sodium phosphate buffer (pH 7.0), 0.1 mM EDTA-Na_2, and 1 % PVP. The homogenate was centrifuged at 12,000*g* for 30 min at 4 °C.

Superoxide dismutase (SOD, EC 1.15.1.1) activity was determined according to the method of Parida et al. (2004) that spectrophotometrically measures inhibition of the photochemical reduction of nitro blue tetrazolium (NBT) at 560 nm. One unit of SOD activity was defined as the amount of enzyme required to cause a 50 % inhibition of the reduction of NBT.

Catalase (CAT, EC 1.11.1.6) activity was determined by the method of Parida et al. (2004). The assay mixture consisted of 0.1 mL enzyme extract, 0.1 mL H_2O_2 and 2.8 mL phosphate buffer (pH 7.0) with 2 mM EDTA. The CAT activity assay is based on the spectrophotometric measurement of H_2O_2 absorbance decrease at 240 nm.

Guaiacol peroxidase (POD, EC 1.11.1.7) activity was assayed according to method of (Farooq et al. 2013) with some modification. The reaction mixture comprised of 0.1 mL enzyme extract, 0.1 mL guaiacol, 0.1 mL H_2O_2 and 2.7 mL 25 mM phosphate buffer (pH 7.0) with 2 mM EDTA. POD activity was determined by measuring the absorbance changes at 470 nm.

Lipid peroxidation and electrolyte leakage

Lipid peroxidation in the tissue of peanut was estimated from the amount of malondialdehyde (MDA) production using the method of Sairam and Srivastava (2001). Fresh leaf and root samples (0.5 g) were homogenized with 10 % trichloroacetic acid and centrifuged with lower speed for 10 min at 4 °C. The supernatant was assayed for MDA according to Shen et al. (2010a, b).

Table 1 Effect of silicon on the root surface area (RSA), average root diameter (RD), root dry weight (RDW), shoot dry weight (SDW) and the root:shoot ratio (R/S) of peanut seedlings under Al stress

Treatment	RSA (cm^2/plant)	RD (cm/plant)	RDW (g)	SDW (g)	R/S
Control	6.990 ± 0.622 a	0.520 ± 0.024 c	0.042 ± 0.001 a	0.641 ± 0.051 a	0.066 ± 0.006 a
Si	6.785 ± 0.535 a	0.531 ± 0.031 c	0.038 ± 0.002 a	0.552 ± 0.042 ab	0.069 ± 0.005 a
Al	3.945 ± 0.451 c	0.681 ± 0.066 a	0.020 ± 0.001 b	0.424 ± 0.024 b	0.047 ± 0.003 b
Al + Si	5.111 ± 0.462 b	0.609 ± 0.053 b	0.036 ± 0.002 a	0.545 ± 0.073 ab	0.066 ± 0.002 a

Different letters within columns indicate a significant difference

Five plants were cut into leaves and root to determinate the electrolyte leakage with a conductivity meter (EC 215 Conductivity Meter, Markson Science, Inc., Del Mar, CA, USA) according to the method of Lutts et al. (1996).

Determination of plant Al concentration

The dried root, stem and leaf samples (200 mg) were ground to fine powder and fully digested using a HNO_3/$HClO_4$ mixture (4:1, v/v) (Zheng et al. 2005). The content of Al in each sample were determined by ICP-MS (Mass Spectroscopy with Inductively Coupled Plasma, model Elan-6000, Perkin Elmer Corp., Norwalk, CO, USA).

Digestion and determination of plant Si concentration

The dried sample of root, stem and leaf were ground to fine powder and digested in a mixture of nitric acid:hydrogen peroxide:hydrofluoric acid (3:3:2, v/v/v). Then, the digested samples were diluted to a constant volume (100 mL) with 4 % boric acid. Silicon concentration in the digested solution was determined using the colorimetric molybdenum blue method described in Ma et al. (2007).

Statistical analysis

Data presented were analyzed using variance (ANOVA) procedure in StatView software (SAS, 2001, SAS Institute, Cary, NC, USA). Results are averages of three independent assays with four replications each. Means were compared using LSD at the 5 % level.

Results

Plant growth and development

The mean root diameter increased by 31.0 % after Al exposure but decreased by 10.6 % with Si application (Table 1). However, the root surface decreased 43.6 % with Al treatment and increased by 29.6 % with Si under Al stress (Table 1). Also, the root dry weight decreased by 52.4 %, shoot dry weight by 33.9 % and R/S by 28.9 % under Al stress while they increased by 80.0, 28.3 and 40.4 % with Si treatment (Table 1).

Antioxidant enzymes

The CAT activity in leaves and roots intensified by 161.6 and 149.0 % with Al treatment compared with 17.0 and 9.0 % with Si. Under combined Al stress and Si treatment, it decreased by as much as 56.3 and 39.0 %, respectively (Fig. 1). The SOD activity in leaves and roots rose slightly (9.1 and 3.0 %) with Si but increased significantly (141.7 and 147.0 %) with Al treatment. Under Al stress, the SOD activity slowed significantly by 36.2 in leaves and 35.0 % in roots with Si application (Fig. 1). The POD activity in leaves and roots increased considerably by 62.0 and 64.1 % with Al treatment. In contrast, peroxidase activities decreased with Si application, especially under Al stress (Fig. 1).

Lipid peroxidation and electric conductivity

Malondialdehyde (MDA) was used to determine lipid peroxidation in leaf and root tissues. The MDA content in leaves and roots which increased by 36.7 and 42.1 % with Al treatment was reduced by 26.0 and 28.2 % with Si under Al stress (Fig. 2). Membrane stability of leaf and root tissues was significantly impaired after Al exposure (Fig. 2). The leakage of electrolytes in leaves and roots increased by 34.5 and 45.0 % with Al treatment compared with 9.4 and 10.4 % after Si application. Under Al stress, the leakage of electrolytes decreased significantly by 15.4 and 25.6 % with Si application.

Gas exchange attributes

The net rate of photosynthetic (P_N), stomatal conductance (Sc), intercellular CO_2 concentration (Ci) and transpiration rate (Tr) were adversely affected by Al treatment (Table 2). The mean P_N decreased by 22.0 %, Sc by 33.3 %, Ci by 14.2 % and Tr by 28.2 %, respectively, after Al exposure. These reductions were reversed by 18.3, 30.0, 17.3 and 21.6 %, respectively, following Si treatment.

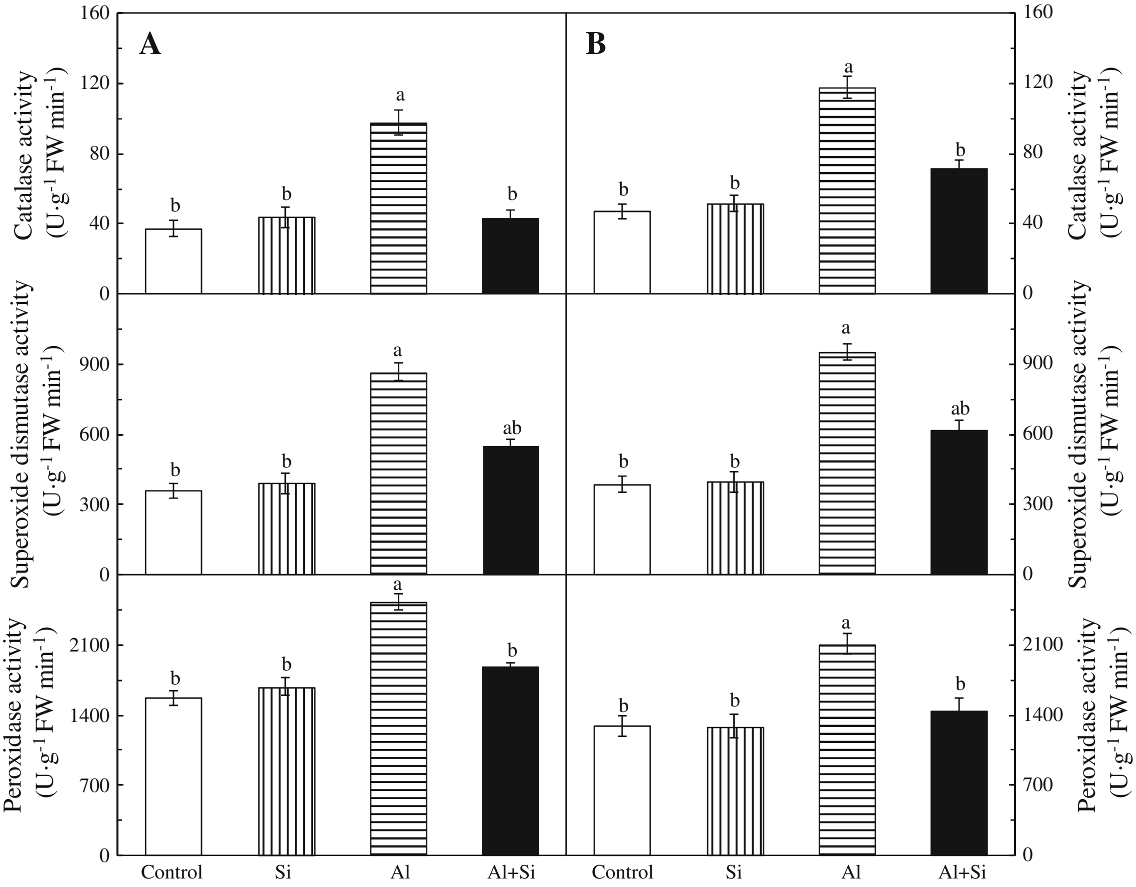

Fig. 1 Effect of silicon on the activities of catalase, superoxide dismutase, and peroxidase in leaf (**a**) and root (**b**) of peanut seedlings under Al stress

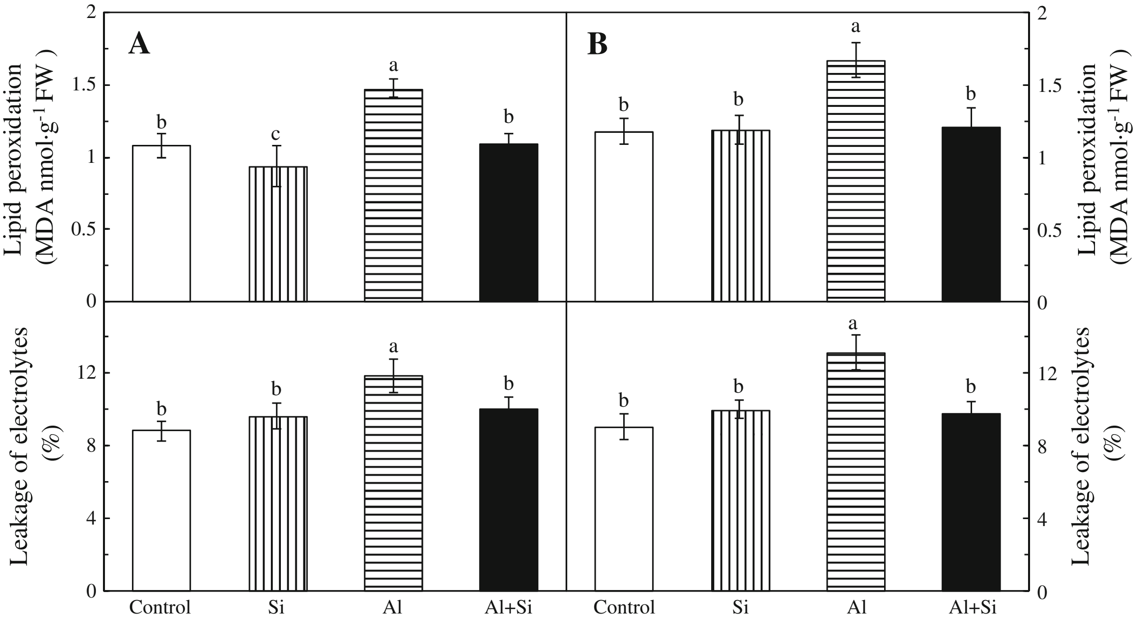

Fig. 2 Effect of silicon on lipid peroxidation and leakage of electrolytes in leaf (**a**) and root (**b**) of peanut seedlings under Al stress

Table 2 Effect of silicon on the net rate of photosynthetic (P_N), stomatal conductance (Sc), intercellular CO_2 concentration (Ci) and transpiration rate (Tr) of peanut seedlings after a week of Si and Al treatment

Treatment	P_N (μmol CO_2 m^{-2} s^{-1})	Sc (mmol H_2O m^{-2} s^{-1})	Ci (μmol CO_2 m^{-2} s^{-1})	Tr (mmol H_2O m^{-2} s^{-1})
CK	9.68 ± 0.23 a	44.5 ± 0.2 a	325.4 ± 3.7 a	4.12 ± 0.12 a
Si	9.60 ± 0.15 a	42.0 ± 0.4 a	319.7 ± 2.4 a	3.96 ± 0.08 a
Al	7.55 ± 0.24 c	29.7 ± 0.5 c	279.2 ± 2.8 c	2.96 ± 0.06 c
Al + Si	8.93 ± 0.60 b	38.6 ± 0.4 b	327.6 ± 4.4 b	3.60 ± 0.09 b

Different letters within columns indicate a significant difference

Table 3 The content of aluminum and silicon in peanut seedlings after a week of Si and Al treatment

Treatment	Content of aluminum (mg g^{-1})			Content of silicon (μg g^{-1})		
	Root	Stem	Leaf	Root	Stem	Leaf
CK	1.37 ± 0.08 d	1.10 ± 0.08 a	1.56 ± 0.06 b	7.11 ± 0.40 c	7.24 ± 0.40 c	9.72 ± 0.58 b
Si	2.95 ± 0.21 c	1.16 ± 0.04 a	1.41 ± 0.09 b	9.93 ± 0.47 a	12.18 ± 0.33 a	13.69 ± 0.32 a
Al	6.46 ± 0.15 a	1.33 ± 0.06 a	2.15 ± 0.07 a	8.11 ± 0.42 b	7.86 ± 0.57 c	9.45 ± 0.60 b
Al + Si	3.83 ± 0.10 b	1.26 ± 0.08 a	1.60 ± 0.03 b	9.19 ± 0.30 ab	10.06 ± 0.30 b	10.66 ± 0.35 b

Different letters within columns indicate a significant difference

Aluminum and silicon contents

The content of aluminum was significantly increased by 371.5 % in the root, 20.9 % in the stem and 37.8 % in the leaf, following Al treatment (Table 3). When Si treatment was imposed on the Al-stressed seedlings, the uptake of Al decreased in the root, stem and leaf by 40.7, 5.3 and 25.6 %, respectively. The content of silicon significantly increased in the root, shoot and leaf with Si application, but under Al treatment it increased most remarkably in the leaf (Table 3).

Discussion

Toxic effects of Al on plant growth manifest through alterations in the growth of roots and shoots, which may invariably reduce root and shoot dry matter (Table 1). The reduction in root and shoot biomass after Al exposure has also been reported (Ryan et al. 1993; Yamamoto et al. 2001). The main symptom of Al toxicity is a rapid inhibition of root growth (Ryan et al. 1993). Cocker et al. (1998) showed that Al toxicity affected the growth and physiological parameters of wheat. The reduction of root surface possibly contributed to the low biomass under enhanced Al stress. The present study suggested that silicon may alleviate Al stress on peanut growth as reported previously for sorghum (Hodson and Sangster 1993), barley (Hammond et al. 1995), wheat (Cocker et al. 1998) and maize (Kidd et al. 2001; Wang et al. 2004). Hammond et al. (1995) also reported that the amelioration of barley root length decrease due to Al stress was achieved using 2.8 mM Si and the application of Si reduced Al uptake into the roots. Changes in biomass allocation due to Al stress are potentially of ecological importance. The root/shoot ratio decreased under Al stress may lead to water deficit stress but application of Si may help to offset this effect on the peanut.

Aluminium treatments significantly impaired peanut growth and development by inhibiting P_N, Sc, Ci and Tr (Table 2). These inhibitions are consistent with previous reports (e.g., Zhang et al. 2007; Aftab et al. 2010), some of which indicated that Al toxicity disturbed the physiological and biochemical processes in plants (Hossain et al. 2004; Zhang et al. 2007; Du et al. 2010). One of the main processes underlying Al-induced stress effects on plants is the increased formation of ROS. Although Al does not generate ROS directly, it produces an oxidative burst (hence, lipid peroxidation) by interfering with the antioxidant defense system that moderates the MDA contents (Yamamoto et al. 2001; Zhang et al. 2007).

Silicon markedly alleviated Al-induced reduction in biomass and photosynthetic parameters in peanut in this study. The alleviating effects of silicon on stresses like diseases, drought, salinity, heavy metals, UV-B radiation, etc. have been intensively studied (Peaslee and Frink 1969; Ma 2004; Eneji et al. 2005; Liang et al. 2007; Kaya et al. 2009; Shen et al. 2009, 2010a, b). Aluminium accumulation in the stressed peanut was greatest in the root, and less in the stem and leaf. Most plants with the highest resistance take up heavy metal by their roots, but lower metal contents was transported to the above-ground parts of the plants. It was reported by many scientists that silicon application would enhance tolerance of toxic metals by reducing the uptake and translocation of metals, including Zn, Mn, Cd, and Al (Kaya et al. 2009; Aftab et al. 2010; Shi et al. 2010; Farooq et al. 2013).

Increased reactive oxygen species (ROS) was found under Al stress as indicated by MDA and electrolyte leakage. Plants generally face oxidative damage when exposed to Al and other metals (Cocker et al. 1998; Wang et al. 2004; Kaya et al. 2009; Shi et al. 2010; Farooq et al. 2013). To counter such an oxidative damage, plants have developed a complex antioxidant system. The antioxidant enzymes such as SOD, POD and CAT in roots and leaves decreased after Al exposure (Fig. 1). Alleviation of metals toxicity by Si was also related with protection against oxidative damage caused by stress. Farooq et al. (2013) has reported that Si alleviated cadmium (Cd) stress in cotton by preventing oxidative damage. According to Wang et al. (2004), amelioration of aluminum toxicity in maize plants was induced by Si application. In this study, the application of silicon was markedly beneficial by reducing lipid peroxidation and electric conductivity and enhancing antioxidant activities of CAT, SOD and POD under Al stress. Therefore, it might be suggested that silicon application could notably increase plant defense system against oxidative damage resulted by Al toxicity.

Conclusion

In present study, aluminum toxicity decreased the growth, biomass, and photosynthetic characteristics of peanut through the formation of reactive oxygen species (ROS) and lowering antioxidant enzyme activities. However, the application of Si significantly reversed these trends, suggesting that Si application can improve Al-toxicity tolerance in peanut.

Author contribution Xuefeng Shen carried out the experiment and prepared the draft. Yong Chen planned the experiment and revised the manuscript. Xueming Xiao helped measurements of Al and Si contents. Zhaoxia Dong helped in drafting the manuscript.

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