Trees (2020) 34:469–481
https://doi.org/10.1007/s00468-019-01929-z

ORIGINAL ARTICLE

Silicon dioxide nanoparticles improve plant growth by enhancing antioxidant enzyme capacity in bamboo (*Pleioblastus pygmaeus*) under lead toxicity

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Received: 15 January 2019 / Accepted: 6 November 2019 / Published online: 18 November 2019
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Abstract

Tissue culture experiments were performed to investigate the impacts of silicon dioxide nanoparticles (SiO_2 NPs) on the improvement of plant growth and development in a bamboo species (*Pleioblastus pygmaeus*) under an experimentally controlled condition contaminated with phytotoxic levels of lead (Pb). Fifteen treatments were administered in the primary trial consisting of 50 µM, 250 µM, 500 µM, 1000 µM, or 1500 µM $PbSO_4$ without and with 100 µM or 500 µM SiO_2 NPs. The results showed that antioxidant enzyme activity first increased at low levels of Pb and then decreased with increasing concentrations of Pb. The addition of SiO_2 NPs increased the capacity of the antioxidant enzymes superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR) and phenylalanine ammonia-lyase (PAL) in plants under Pb stress. Additionally, our findings indicated that SiO_2 NPs may protect the bamboo plant plasma membrane and preserve the integrity of cells against Pb-induced oxidative stress by reducing the contents of hydrogen peroxide (H_2O_2) and soluble protein (SP), and polyphenol oxidase (PPO) activity. Regarding impacts on indexes of plant photosynthesis, the results revealed that SiO_2 NPs were able to regulate plant growth by increasing chlorophyll and carotenoid contents, which led to increased plant biomass and plant dry weight under Pb toxicity. We conclude that SiO_2 NPs improve plant growth (plant biomass) by increasing antioxidant enzyme capacity in bamboo under Pb stress. Our results also revealed that 500 µM SiO_2 NPs was much more effective than 100 µM SiO_2 NPs at maintaining plant growth under Pb toxicity.

Keywords Silicon dioxide nanoparticles (SiO_2 NPs) · Lead (Pb) · Bamboo · Antioxidant capacity · Photosynthesis indexes · Plant biomass

Introduction

Among heavy metals, Pb is one of the most hazardous metals in air and soil and poses a major threat to human health and life (Krzesłowska et al. 2016; Li et al. 2016). The root surfaces of plants are one of the main absorption sites of lead, which can bind Pb to carboxylic acid forms of mucilage uronic acids. (Peralta-Videa et al. 2009). An excess of Pb in plants stimulates ROS production in the cell wall, which disrupts cell processes such as cell signaling and cell adhesion by affecting ion balance and superseding vital ions in cells (Lyer et al. 2015). Additionally, in cell nuclei, Pb binds DNA, impacts mitosis, prolongs interphase, and increases the time required for the cell cycle (Dikilitas et al. 2016). Regarding plant morphology, Pb inhibits root and shoot growth and increases the level of suberin in the roots (Salazar et al. 2016). In photosynthesis, Pb impacts the

Communicated by S. Merkle.

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antenna and photoreaction center, which inhibits photosystem II and consequently decreases photosynthetic capacity in the plant under metal stress (Dao and Beardall 2016).

Silicon, the second most abundant element in the Earth's crust, is beneficial for plant growth and development (Shi et al. 2005a, b; Liang et al. 2007). It has been reported that silicon can increase plant resistance in various species by ameliorating heavy metal stress(Liang et al. 2001; Neumann and Zur Nieden 2001; Rogalla and Römheld 2002;Liang et al. 2005)and is an ameliorator of abiotic stress in higher plants (Liang et al. 2003, 2005). The alleviating effects of silicon nanoparticles on heavy metal toxicity in plants are achieved through both external and internal mechanisms as follows: (1) externally, silicon forms complexes with toxic metals outside the root, resulting in the reduced availability and uptake of metal ions by the plant; (2) internally, silicon alters cell wall composition to control metal ion transport across the plasma membrane, enhances vacuolar compartmentalization of metal ions, synthesizes complexes with metals and eventually induces antioxidant enzyme activity within the plant. (Tubana and Heckman 2015). These mechanisms can maintain ROS at low levels, regulate the redox signaling network and increase plant resistance, allowing plant development to withstand ROS accumulation (Potters et al. 2010; Foyer and Noctor 2011).

In recent years, nanoparticles have been widely used to improve human life in different fields (Geiger 2009; Karimi and Mohsenzadeh 2016). Nanoparticles exist in three dimensions with sizes of between 1 and 100 nm and either molecular or atomic aggregates (Whitesides 2005; Karimi and Mohsenzadeh 2016). Among various types of nanoparticles, SiO_2 NPs are well documented to stimulate plant growth and ameliorate stress in various plant species (Baoshan e al., 2004; Yuvakkumar et al. 2011; Haghighi et al. 2012; Suriyaprabha et al. 2012; Slomberg and Schoenfisch 2012; Siddiqui and Al-Whaibi. 2013). Yuvakkumar et al. (2011) reported that SiO_2 NPs can increase seed germination, chlorophyll indexes and water balance efficiency in *Zea mays*, while Haghighi et al. (2012) reported a reduction in the damaging impacts of salt stress on the growth indexes of tomato seedlings by using SiO2 NPs. Bao-shan et al. (2004) exposed potato roots to various SiO_2 NP concentrations (60 µM, 125 µM, 250 µM, 500 µM, 1000 µM, and 2000 µM) and reported that the SiO_2 NPs improved growth indexes of the potatoes, concluding that 500 µM SiO_2 NPs induced the highest plant growth.

Bamboo (*Bambusoideae*) plants, occupying more than 6 million hectares of Chinese forestlands, are a rich source of nutrients and provide livelihood as well as medicine for a large number of local families in southern and western China (Hogarth and Belcher 2013). *Pleioblastus pygmaeus* is an evergreen dwarf bamboo with a height of about 30–50 cm, which is used for gardening and landscaping. It is in leaf all year around and can grow in acidic, neutral and basic (alkaline) soils. Heavy metal contamination (frequently Pb, Cu, and Zn) caused by anthropogenic activities is one of the major problems in the agricultural forestlands in the south-west regions of China (Zhang et al. 2015). Therefore, it is important to find appropriate applications to improve bamboo plant growth and development under heavy metal toxicity. This need has led to the selection of silicon as the ameliorating factor in this study. Bamboo stands can accumulate silicon in the form of amorphous silicon (Umemura and Takenaka 2014). However, there is a lack of knowledge regarding the impact of silicon nanoparticle forms on bamboo species under heavy metal stress. The aims of this paper were the following: (1) evaluate the impact of SiO_2 NPs on antioxidant enzyme activity of bamboo plant under various concentrations of Pb and (2) determine the optimum levels of SiO_2 NPs that can increase plant growth and biomass under toxic metal conditions.

Materials and methods

Plant material and growth conditions

Ten mm-long nodal explants were collected from 1-year-old branches of a single clone of *P. pygmaeus,* which has been growing in the bamboo garden of Nanjing Forestry University since 1982. To induce axillary shoot production and proliferation, explants were cultured on MS medium (Murashige and Skoog 1962) supplemented with 4 µM 6-benzylaminopurine (6-BA) and 0.5 µM kinetin (KT), together with 30 g/L sucrose, and 7–10 g/L agar. The roots were induced from the proliferated young shoot. For this purpose, MS medium, placed in 60-mm-diameter glass Petri dishes in an incubator, was supplemented with 1.2 µM of thiamine–HCl, 4 µM of nicotinic acid, 0.6 mM of myo-inositol, 3 µM of pyridoxine, 30 g/L sucrose, and 7–10 g/L agar and was adjusted to pH 5.8 ± 0.1 in which 0.1 mg/L IAA was used as growth hormone regulator. The MS medium was sterilized in a microwave oven at 120 °C for 30 min. Then, the plantlets were transferred to the tissue culture chamber to grow as research materials (Fig. 1).

The treatments consisted of five replicates of each of five concentrations of $PbSO_4$ (50 µM, 250 µM, 500 µM, 1000 µM, and 1500 µM) alone or with two concentrations of SiO2 NPs (100 µM and 500 µM). After preparing 1 L of medium, 30 g of sucrose with different concentrations of Pb in combination with different concentrations of SiO_2 NPs was added to the solution and then the pH was adjusted to 5.8. Next, an adequate amount of agar was added, and the solution was transferred to a microwave oven for 10 min. The solution was sterilized in an autoclave (HiClave HVE-50). The bamboo plant was placed in glass Petri dishes (60 mm

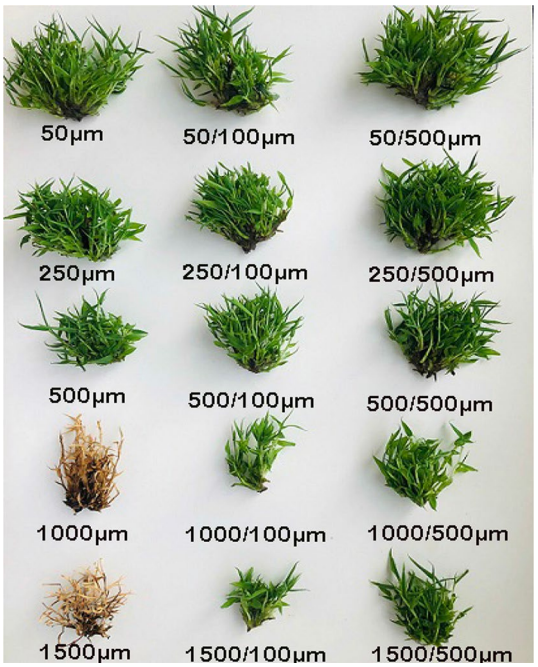

Fig. 1 Bamboo species (*Pleioblastus pygmaeus*) as affected by different Pb concentrations (50 µM, 250 µM, 500 µM, 1000 µM, and 1500 µM) in combination with 100 µM and 500 µM SiO_2NPs application levels

diameter and 90 mm height) containing 100 mL culture medium in the ultraviolet-sterilized inoculation incubation hood (Air Tech) with white fluorescent lamps (wavelength 350–750 nm) at 25 °C for 4 h. The pre-incubated bamboo plants were then transferred to and maintained in a plant tissue culture chamber with the same light source and intensity as in the incubator, a photoperiod of 16 h and temperatures of 30/25 °C and 17/22 °C during the light and dark periods, respectively, for 25 days. These growth conditions mimicked those of natural environment typically experienced by the bamboo plant in its habitat. The SiO_2 NPs were provided by Nanjing Jiancheng Company in Jiangsu Province, China. The SiO_2 NPs were a 95% pure nano silica powder. NPs were approximately 20 nm and had a spherical shape. The concentrations of Pb and SiO_2 NPs were chosen according to the preliminary studies conducted by our research group that established high and low levels within the tolerance range of the bamboo species (Fig. 2).

After the end of the incubation period, the samples collected from the bamboo shoot were sent to the laboratory for analysis. The antioxidant enzyme activities, including the activities of superoxide dismutase (SOD), catalase (CAT), glutathione reductase (GR) and phenylalanine ammonia-lyase (PAL), were thoroughly measured. Total soluble protein (Sp), hydrogen peroxide (H_2O_2) and polyphenol oxidase (PPO) levels were estimated. Then, chlorophyll a, chlorophyll b, total chlorophyll and carotenoid contents were calculated. After measuring the indexes, the biomass of the bamboo sample was determined based on the dry weight (DW) of the shoots and roots.

Sampling

To prepare for the experiment, 0.5 g of the sample (leaves) was carefully cut with scissors. After checking the weight, the samples were pulverized following the exposure to liquid nitrogen, which quickly froze the samples. This was followed by crushing the samples using mortar and pestle. After thawing, the samples were preserved at 2–8 °C. Then, 2 mg pH 7.8 phosphate buffer was added to the resulting powder in the test tube. The samples were centrifuged for 20 min at the optimum speed of 2000–3000 RPM and then the supernatant was removed.

Antioxidant activities

Superoxide dismutase enzyme activity (SOD, EC 1.15.1.1) was quantified based on photoreduction in nitro blue tetrazolium (NBT) according to the method of Zhang (1992). In this method, the SOD content was determined by using the following materials: 1 g/50 mL MET, 0.01 g/100 mL rib, 0.1 g/1000 mL NBT, and 2.1 g/100 mL EDTA. To quantify soluble SOD in the samples, 0.2 mL MET, 0.2 mL NBT, 0.2 mL Rib, 0.2 mL EDTA, and 3.1 mL pH 7.0 buffer as well as 0.1 mL of the sample were added to a test tube. Then, in the next stage, the test tubes were exposed to light for 10–20 min. After changing color, the soluble samples were transferred to a spectrometer for OD measurement. Catalase (CAT, EC 1.11.1.6) activity was determined based on two H_2O_2 reactions analyzed at 240 nm. According to Aebi's method (Aebi 1984), the soluble samples were prepared by adding 1.6 mL water, 1 mL Tris–HCl, and 0.2 mL H_2O_2 to 0.1 mL sample, and then the soluble sample was measured two or three times at 230 nm by a spectrometer (Beijing Purkinje TU-1810 UV–vis Spectrometer) to determine the CAT content. Glutathione reductase (GR) was quantified by using a commercial chemical assay kit (Nanjing Jiancheng Company). For this experiment, the material used consisted of 0.5% (w/v) Triton-100, 0.1 mm EDTA, and 2% PVP, which were added to the sample. The mixture was centrifuged at 10,000 RPM and 4 °C for 10 min. For the determination of bamboo concentration or the analysis of enzyme activity, the supernatant was quantified based on the manufacturer's instructions.

Phenylalanine ammonia-lyase (PAL) activity was assessed based on the method of Cai et al. (2008). The leaf samples from our experiment (0.5 g) were homogenized with a mortar and pestle. Then, the samples were placed in an ice bath containing 5 mL 50 mM borate buffer (pH 8.8) with 1 mM EDTA and 5.0 mM thioalcohol. The homogenate

Fig. 2 Root induction from the proliferated young shoot in bamboo species (*Pleioblastus pygmaeus*)

was centrifuged at 13,000 RPM for 10 min at 4 °C. Then, the reagents, including 2 mL 50 mM borate buffer (pH 8.8) and 1.0 ml 20 mM L phenylalanine, were added to 0.2 mL crude homogenate, which was termed as the reaction mixture. Then, the reaction mixture was incubated for 30 min at 40 °C and fixed by exposure to 0.25 mL 5 M HCl. Then, the increase in absorbance at 290 nm was measured with the spectrometer.

Hydrogen peroxide (H_2O_2), soluble protein (SP), and polyphenol oxidase (PPO)

To determine the concentration of hydrogen peroxide (H_2O_2), the chemical reaction from a commercial assay kit (Nan Jing Jian Cheng Company) was employed. To determine the H_2O_2 content, the tissue was prepared by cutting leaf discs from the treated leaves and submerging them in liquid nitrogen (LN2) until the beginning of the analysis. Storage at higher temperatures (− 80 °C or − 20 °C) resulted in the loss of as much as 60% of the H_2O_2 within 7 days. For analysis, the samples were removed from the LN2 and then quickly weighed without thawing. Then, the samples were ground under LN2 with a prechilled mortar and pestle. In the next step, a modified ferrous ammonium sulfate/xylenol orange (FOX) method was used to estimate the content of H_2O_2 in the extracts. The soluble protein content was measured based on the change in protein concentration with Coomassie Brilliant Blue (G25). According to the Bradford method (Bradford 1976), a soluble protein test was conducted in 50 mL 90% ethanol, 0.1 Coomassie Brilliant Blue

G25, 100 mL H_3PO_4, and 1000 mL water. After preparation, the soluble samples were transferred to a spectrometer to determine the content of soluble protein. Polyphenol oxidase (PPO) was quantified with the method of Cai et al. (2008). A 0.25 g sample was homogenized and placed in an ice bath with 5 ml 50 mM borate buffer (pH 8.7) containing 0.1 g PVP and 5.0 mM sodium hydrogen sulfite. Then, the soluble sample was centrifuged at 13,000 RPM for 10 min at 4 °C. The final soluble samples were obtained by combining 0.1 mL of the final mixture with 3 mL of a solution including 0.5 mL 0.15 mM catechol and 50 mM potassium phosphate buffer (pH 6.5). In the next step of determining polyphenol oxidase (PPO) activity, the soluble samples were measured at 420 nm with a spectrophotometer for 10 min at 30 °C (Gauillard et al. 1993).

Measurements of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids

Chlorophyll a, chlorophyll b, and carotenoids were quantified according to the method of Arnon (1949). According to this method, a 0.5 g leaf sample was ground in a porcelain mortar, pulverized in liquid nitrogen, and squeezed to prepare liquid sample extract. Then, 20 ml 80% acetone was added to the sample at 0 to 4 °C. Then, the sample was transferred for centrifugation at 6000 RPM for 10 min. In the next step, the supernatant was transferred to a glass balloon. In the final step, some samples were placed inside the balloon in a cuvette of the spectrophotometer, and the absorbance of each sample was determined by a spectrophotometer at 663 nm for chlorophyll a content, 645 nm for chlorophyll b content, and 470 nm for carotenoid content. After calculating the indexes, we used the following formulas, in which the levels of chlorophyll a, b, and carotenoids are in mg/g fresh weight:

$$\text{Chlorophyll a} = (19.3 \times \text{A663} - 0.86 \times \text{A645})\, V/100W,$$

$$\text{Chlorophyll b} = (19.3 \times \text{A645} - 3.6 \times \text{A663})\, V/100W,$$

$$\text{Carotenoids} = 100\,(\text{A470}) - 3.27(\text{mg chl. a}) - 104(\text{mg chl. b})/227,$$

where V is the volume of the filtered solution (supernatant obtained from centrifugation); A is the absorbance at 663, 645, or 470 nm; and W is the fresh weight of the sample in grams.

Biomass determination

After exposure to SiO_2 NPs-Pb, the plant roots and shoots were carefully cleaned and washed with deionized water. All surface water was removed by oven drying (vacuum dry ovenDZF-6090). Sample fixation was conducted at 110 °C for 20 min. The treated samples were then dried at an optimum temperature of 80 °C to a constant dry weight. The dry weight represented our experimental biomass and was determined for five replicates in each treatment.

Statistical analysis

The experiment was performed using a completely randomized design (CRD) arranged in a two-way factorial layout with five replicates. Analysis of variance (ANOVA) was carried out with the statistical software package R. The mean differences were compared using Tukey's test at the $p < 0.05$ probability level.

Results

The effect of Pb–(SiO_2 NP) combination treatment on antioxidant enzyme activities

The results obtained by comparing the average change in antioxidant enzyme activities (SOD, CAT, PAL, and GR) showed that there was a significant difference among the different concentrations of Pb–(SiO_2 NPs) ($p < 0.001$). According to Fig. 3, in almost all indexes, the response curve of antioxidant enzyme activity was in the shape of a curve. Thus, there was a significant increase at low concentrations and then a decrease with increasing concentrations, indicating Pb toxicity. As shown in Table 2, the greatest increases in antioxidant activity occurred at 250 µM and 500 µM Pb; the activities of the enzymes SOD, CAT, PAL, and GR first increased with 250 µM and 500 µM Pb and then decreased with high levels of Pb (1000 µM and 1500 µM Pb). However, the evaluation of SiO_2 NP treatment in combination with Pb revealed the triggering effect of SiO_2 NPs on enzymatic activity; with increasing levels of SiO_2 NPs, the antioxidant activities of all the indicator enzymes increased. In this case, the results indicated that the highest levels of antioxidant activity were associated with 500 µM Pb + 500 µM SiO_2 NPs in three indexes; CAT, GR, and PAL activity increased by 48%, 53%, and 35%, respectively. Additionally, SOD was impacted by treatment with 250 µM Pb + 500 µM SiO_2 NPs, showing a 31% increase in antioxidant activity (Table 2). The results indicated that $SiNO_2$ NPs had less of an effect at the high concentrations of Pb; the antioxidant enzyme activities remained constant at 1000 µM and 1500 µM Pb. In many cases, there was no significant difference between treatments, demonstrating the remarkable reduction in SiO_2 NP efficiency at high concentrations of Pb. In general, the results indicated that GR activity was influenced the most by the addition of SiO_2 NPs, with an increase of 1.24-fold. PAL, CAT, and SOD activity increased by 1.17-, 1.15-, and

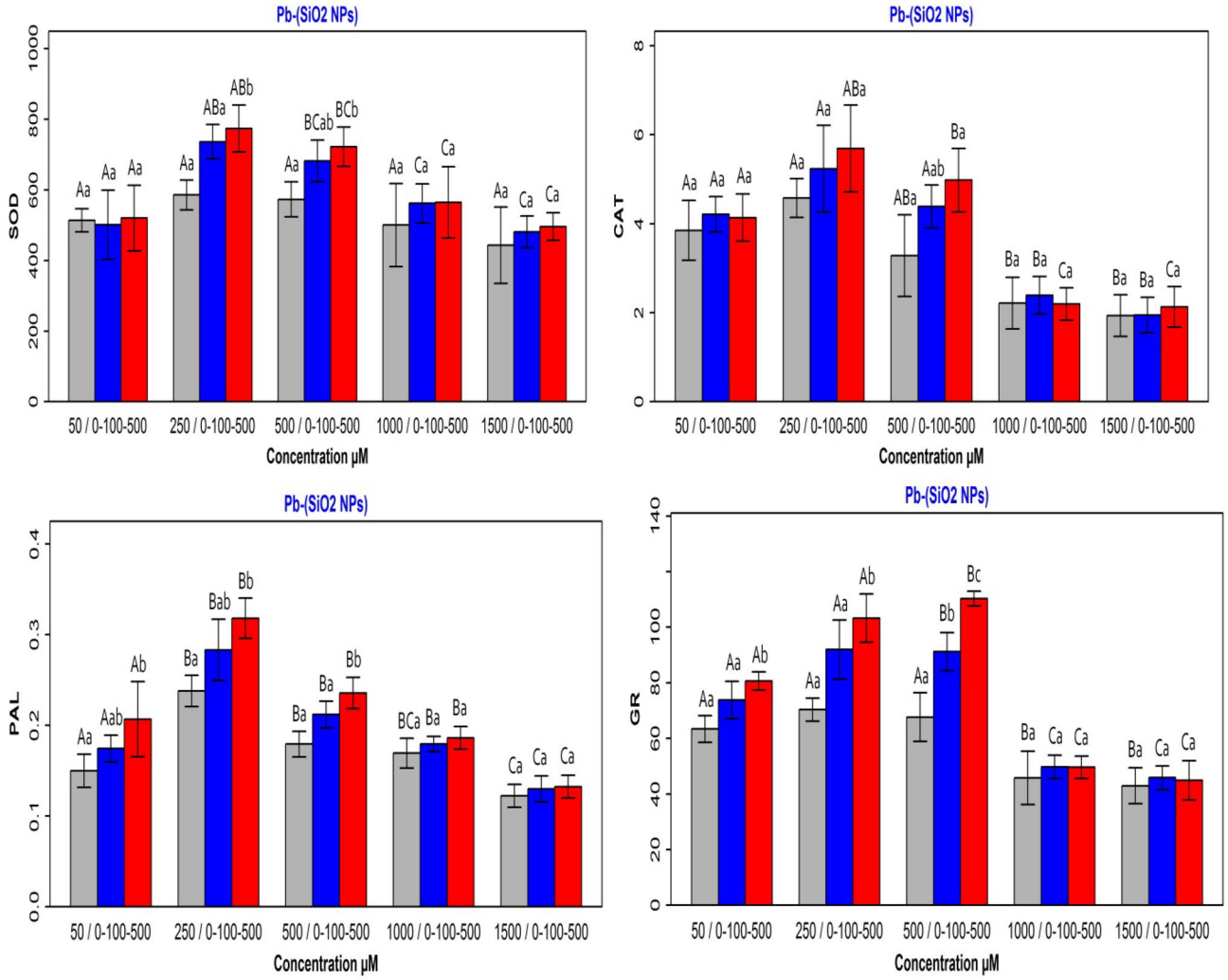

Fig. 3 Effects of the combination of Pb–(SiO_2 NPs) on antioxidant enzymes activities of *Pleioblastus pygmaeus*. The treatments included different concentrations of Pb alone or in combination with various levels of SiO_2 NPs (100 µM and 500 µM). The capital letters indicate statistically significant differences across different concentrations of Pb treatment alone or in combination with SiO_2 NPs (the bars with the same colors), while the lowercase letters indicate statistically significant differences within each concentration of Pb treatment alone or in combination with SiO_2 NPs (the bars with different colors) according to Tukey's test ($p < 0.05$)

1.14-fold, respectively, in the presence of SiO_2 NPs across all the tested Pb concentrations.

The effect of Pb–(SiO_2 NP) combination treatment on the content of hydrogen peroxide (H_2O_2), soluble protein (SP), and polyphenol oxidase (PPO)

According to Table 1, Pb treatment had the deleterious effect of increasing the levels of free radicals and soluble proteins in plant tissue and inside the cell. This injurious effect was mitigated by adding SiO_2 NPs; however, at higher concentrations of Pb, this reduction was not evident. The data describing the effect of Pb on the indexes of hydrogen peroxide (H_2O_2), soluble protein (SP), and polyphenol oxidase (PPO) indicated a significant linear increase in their contents with increasing Pb levels ($p < 0.01$). Therefore, the highest level of injury was observed at high concentrations of Pb (1000 µM and 1500 µM), while the lowest level of injury occurred at lower concentrations of Pb (50 µM, 250 µM, and 500 µM). However, SiO_2 NPs had a significant role in reducing the deleterious effects of metals; thus, increasing SiO_2 NP levels in combination with Pb decreased the negative and toxic effects caused by Pb. The results indicated that 500 µM SiO_2 NPs were more effective than 100 µM SiO_2 NPs at ameliorating Pb toxicity. As shown in Table 2, the highest percent reduction in the H_2O_2 and SP indexes was observed in the combination treatment of 500 µM Pb + 500 µM SiO_2 NPs, with reductions of 29.1% and 24.7%, respectively, and 250 µM Pb +500 µM SiO_2 NPs resulted in the highest percent reduction in the PPO index, with a 64.7% reduction.

Table 1 The effect of the combination of Pb–(SiO_2 NPs) on the content of hydrogen peroxide (H_2O_2), soluble protein (SP), and polyphenol oxidase (PPO) of *Pleioblastus pygmaeus*

Pb	(SiO_2 NPs)	H_2O_2	SP	PPO
μM	μM	μg/g.Fw	μg/g.Fw	$U\,g^{-1}$
50	− Si	3.7187 ± 1.3391^{Aa}	0.0605 ± 0.0080^{Aa}	0.0480 ± 0.0078^{Aa}
	+ Si 100	2.9512 ± 0.7721^{Aa}	0.0498 ± 0.0045^{Aa}	0.0338 ± 0.0052^{Ab}
	+ Si 500	2.3559 ± 0.4365^{Aa}	0.0498 ± 0.0022^{Aa}	0.0261 ± 0.0067^{Ab}
250	− Si	5.8593 ± 0.8493^{Aa}	0.07256 ± 0.0071^{Ba}	0.0659 ± 0.0054^{ABa}
	+ Si 100	4.1950 ± 0.9661^{Ba}	0.0610 ± 0.0062^{Bab}	0.0410 ± 0.0060^{Ab}
	+ Si 500	4.4056 ± 0.9345^{Ba}	0.0601 ± 0.0047^{Bb}	0.0313 ± 0.0035^{Bb}
500	− Si	8.7956 ± 0.8276^{Aa}	0.0917 ± 0.0041^{BCa}	0.0795 ± 0.0044^{BCa}
	+ Si 100	6.6518 ± 0.6021^{Cb}	0.0722 ± 0.0093^{Cab}	0.0531 ± 0.0029^{Bb}
	+ Si 500	6.222 ± 0.3015^{Cb}	0.0686 ± 0.0147^{Cb}	0.0402 ± 0.0070^{Cc}
1000	− Si	9.3656 ± 0.7506^{Ba}	0.1059 ± 0.0117^{CDa}	0.0989 ± 0.0048^{CDa}
	+ Si 100	8.8425 ± 0.2811^{Da}	0.1053 ± 0.0102^{CDa}	0.0846 ± 0.0054^{BCb}
	+ Si 500	8.9862 ± 0.6929^{Da}	0.1003 ± 0.0027^{CDa}	0.0743 ± 0.0033^{CDc}
1500	− Si	10.9046 ± 1.2132^{Ba}	0.145 ± 0.0129^{Da}	0.1086 ± 0.0164^{Da}
	+ Si 100	10.5378 ± 0.7120^{Da}	0.135 ± 0.0057^{Da}	0.0936 ± 0.0108^{Ca}
	+ Si 500	10.6950 ± 0.9250^{Ea}	0.145 ± 0.0040^{Da}	0.0996 ± 0.0067^{Da}

Each data point is the mean ± SE of five replicates. The treatments included different concentrations of Pb alone or in combination with various levels of SiO_2 NPs (100 μM and 500 μM). The capital letters indicate statistically significant differences across different concentrations of Pb treatment alone or in combination with SiO_2 NPs, while the lowercase letters indicate statistically significant differences within each concentration of Pb treatment alone or in combination with SiO_2 NPs according to Tukey's test ($P < 0.05$)

Table 2 The percentage of change in antioxidant enzymatic activities under the various concentrations of Pb–(SiO_2 NPs) compared to their control treatments (Pb)

Concentration of Pb–(SiO_2NPs) Combination	SOD	CAT	GR	PAL	PPO	SP	H_2O_2
50 × 100 μM	2.6%	5.5%	17.1%	9.31%	19.63% ↓	17.3% ↓	16.2% ↓
50 × 500 μM	5.7%	10.7%	28.1%	28.43%	39.2% ↓	20% ↓	24.4% ↓
250 × 100 μM	25%	18.29%	35%	12.5%	39.2% ↓	20% ↓	19.3% ↓
250 × 500 μM	31.1%	30.6%	51%	29.1%	64.7% ↓	23.6%↓	24.3% ↓
500 × 100 μM	14.6%	28%	32.8%	23.55%	35.7% ↓	23.7%↓	22.5% ↓
500 × 500 μM	25.8%	48.5%	53.6%	35.29%	49.7% ↓	24.7%↓	29.1% ↓
1000 × 100 μM	9%	5/01%	6.38%	6%	11.3% ↓	6% ↓	5% ↓
1000 × 500 μM	10%	5/01%	6.38%	10.4%	19.2% ↓	6% ↓	5% ↓
1500 × 100 μM	6.6%	3.5%	9.52%	8.33%	14.6% ↓	6.8% ↓	3.2% ↓
1500 × 500 μM	11%	4.3%	7.90%	8.33%	14.6% ↓	6.8% ↓	3.00% ↓

Additionally, the results showed that at $PbSO_4$ concentrations above 1000 uM, SiO_2 NPs did not reduce the deleterious effects of Pb. In general, according to the results, SiO_2 NPs can ameliorate Pb toxicity in this species by reducing the levels of hydrogen peroxide (H_2O_2), soluble protein (SP), and polyphenol oxidase (PPO) by 15.2%, 15.7%, and 30.7%, respectively, compared with their controls.

The effect of Pb–(SiO_2 NP) combination treatment on the content of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids

The results obtained from our photosynthesis index data showed that with increasing concentrations of Pb, the contents of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids were significantly decreased ($p < 0.01$), which demonstrated the negative impact of Pb on the metabolism of this bamboo species. However, the results revealed an increasingly important role of SiO_2 NPs in photosynthesis and plant metabolism. Therefore, with increasing levels of SiO_2 NPs, the contents of chlorophyll and carotenoids increased. Additionally, this increasing trend was considerable at 250 μM and 500 μM Pb in combination with 500 μM SiO_2 NPs. In this study, compared with controls, the most effective SiO_2 NP concentration was 500 μM Pb + 500 μM SiO_2 NPs, which induced a 28% increase in chlorophyll a content, a 50% increase in chlorophyll b content, and a 37% increase in total chlorophyll content. A 12.7% increase

over controls in the content of carotenoids was observed with 250 µM Pb + 500 µM SiO_2 NPs (Table 3). However, at high levels of Pb (1000 µM and 1500 µM), the addition of SiO_2 NPs did not have a significant effect on chlorophyll and carotenoid contents. This result is an indicator of the inhibition threshold of this plant when exposed to nonessential heavy metals such as Pb. In general, in the present experiment, SiO_2 NPs improved the photosynthetic properties of plants under Pb stress by increasing the chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents by 1.12-, 1.21-, 1.14-, and 1.05-fold, respectively, compared with their controls.

The effect of Pb–(SiO_2 NP) combination treatment on the biomass production of shoots and roots

The biomass was determined by measuring the dry weight of plant roots and shoots. These results showed a significant reduction in dry weight with increasing Pb concentration in both shoots and roots ($p < 0.01$) (Fig. 4). Therefore, the highest plant dry weight was observed under treatment with low concentrations of Pb (50 µM–500 µM), with 0.74 g in shoots and 0.99 g in roots; the lowest plant dry weight was observed with high concentrations of Pb (1500 µM), with 0.23 g in shoots and 0.30 g in the roots. These results demonstrated the role of Pb toxicity in the reduction of plant biomass. In contrast, the analysis of the results obtained with the combination treatment of Pb–(SiO_2 NPs) indicated that the SiO_2 NP levels had a significantly positive effect on dry weight of the bamboo plant. The combination of 500 µM Pb with 500 µM SiO_2 NPs showed the largest dry weight of plant shoots and roots, with 1.41- and 1.43-fold increases, respectively, compared with the control. In general, the application of 500 µM SiO_2 NPs had the greatest impact on the increase in dry weight; the increases observed with 500 µM SiO_2 NPs were 21% in the shoot and 26% in the root, while the increases observed with 100 µM SiO_2 NPs were 10% and 13% in the shoot and root, respectively (Table 4).

Discussion

Antioxidant enzymes scavenge ROS in the intercellular organs of plants, such as the chloroplast, cytosol, apoplast, mitochondria, and peroxisomes, through several chemical reactions that involve peroxisomal glutathione peroxidase, water–water, and ascorbate–glutathione (Foyer and Noctor 2011; Hasanuzzaman et al. 2012). This kind of defense mechanism can preserve the integrity of plants, enabling them to cope with metal stress through chloroplasts, mitochondria, and nuclei (Nwugo and Huerta 2008; Song et al. 2009). Among the antioxidant enzymes, SOD plays a role in the first line of ROS scavenging (Takahashi, and Asada 1983), catalyzing the change in superoxide anions to peroxide (Neumann et al. 1997). CAT functions to convert H_2O_2 to water and O_2 (Das and Roychoudhury 2014; Singh et al. 2017). Glutathione reductase (GR, EC, 1.6.4.2) contains disulfide groups (Trivedi et al. 2013) and can regulate the

Table 3 The effect of the combination of Pb–(SiO_2 NPs) on the content of chlorophyll a, chlorophyll b, total chlorophyll, and carotenoids

Pb	(SiO_2 NPs)	Chla	Chlb	T. Chl	Carotenoids
µM	µM	(µg g^{-1} F.w.)	(µg g^{-1} F.w.)	(µg g^{-1} F.w.)	(µg g^{-1} F.w.)
50	− Si	3.710 ± 0.627^{Aa}	2.599 ± 0.065^{Aa}	6.310 ± 0.571^{Aa}	54.525 ± 5.766^{Aa}
	+Si 100	3.920 ± 0.600^{Aa}	3.453 ± 0.280^{Aab}	7.374 ± 0.858^{Aa}	52.45 ± 8.019^{Aa}
	+Si 500	4.131 ± 0.161^{Aa}	3.224 ± 0.445^{Ab}	7.354 ± 0.290^{Aa}	54.43 ± 5.508^{Aa}
250	− Si	3.398 ± 0.262^{Aa}	2.188 ± 0.264^{ABa}	5.587 ± 0.140^{ABa}	49.055 ± 5.279^{Aa}
	+Si 100	3.837 ± 0.249^{Aab}	2.520 ± 0.170^{Bab}	6.358 ± 0.345^{ABa}	48.181 ± 3.416^{Aab}
	+Si 500	4.009 ± 0.309^{Ab}	2.847 ± 0.442^{ABb}	6.788 ± 0.487^{Ab}	55.80 ± 2.085^{Ab}
500	− Si	3.131 ± 0.331^{ABa}	1.863 ± 0.215^{ABa}	4.994 ± 0.492^{BCa}	44.96 ± 9.195^{Aa}
	+Si 100	3.238 ± 0.128^{ABb}	2.367 ± 0.279^{Bab}	5.605 ± 0.348^{BCb}	51.72 ± 3.622^{Aa}
	+Si 500	3.785 ± 0.221^{Ab}	2.779 ± 0.196^{ABb}	6.633 ± 0.558^{Ab}	49.70 ± 5.302^{ABa}
1000	− Si	2.387 ± 0.308^{BCa}	1.940 ± 0.332^{ABa}	4.328 ± 0.115^{CDa}	41.69 ± 7.298^{Aa}
	+Si 100	2.865 ± 0.292^{BCa}	2.095 ± 0.280^{BCa}	4.960 ± 0.374^{CDa}	41.01 ± 7.574^{Aa}
	+Si 500	2.737 ± 0.421^{Ba}	2.237 ± 0.454^{BCa}	4.974 ± 0.208^{Bb}	43.52 ± 5.546^{Ba}
1500	− Si	2.018 ± 0.590^{Ca}	1.617 ± 0.596^{Ba}	3.636 ± 0.480^{Da}	39.185 ± 9.090^{Aa}
	+Si 100	2.117 ± 0.338^{Ca}	1.729 ± 0.187^{Ca}	3.847 ± 0.452^{Da}	40.91 ± 6.881^{Aa}
	+Si 500	2.266 ± 0.462^{Ba}	1.665 ± 0.557^{Ca}	3.932 ± 0.925^{Ba}	40.36 ± 5.378^{Ba}

Each data point is the mean ± SE of five replicates. The treatments included different concentrations of Pb alone or in combination with various levels of SiO_2 NPs (100 µM and 500 µM). The capital letters indicate statistically significant differences across different concentrations of Pb treatment alone or in combination with SiO_2 NPs, while the lowercase letters indicate statistically significant differences within each concentration of Pb treatment alone or in combination with SiO_2 NPs according to Tukey's test ($P < 0.05$)

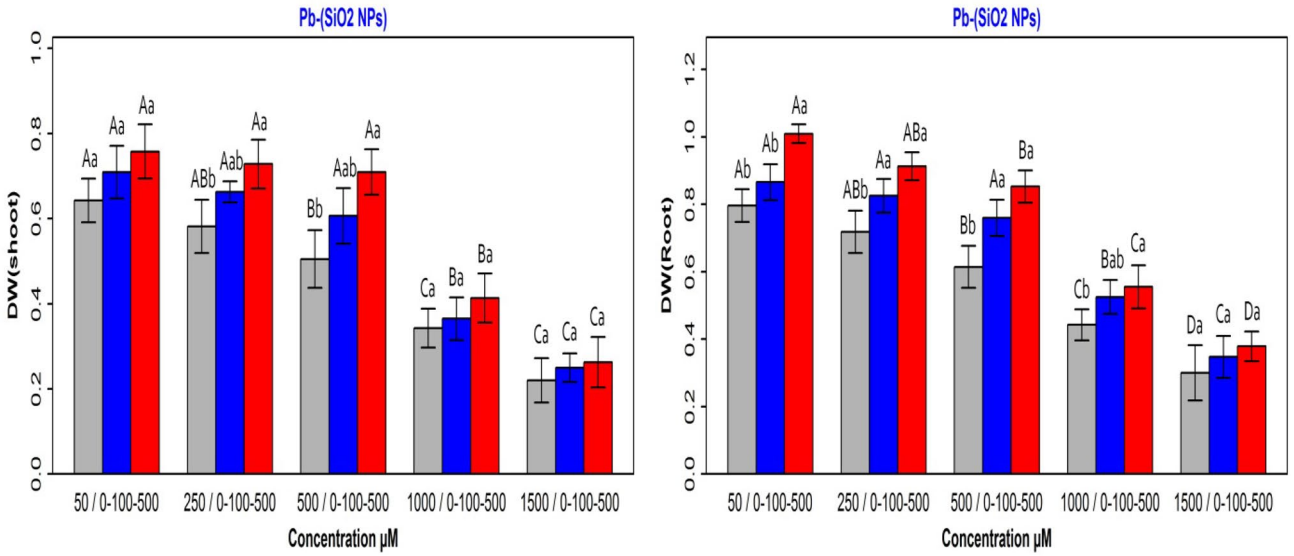

Fig. 4 Effects of the combination of Pb–(SiO_2 NPs) on dry weight (DW) of shoot and root in *Pleioblastus pygmaeus*. The treatments included different concentrations of Pb alone or in combination with various levels of SiO_2 NPs (100 µM and 500 µM). The capital letters indicate statistically significant differences across different concentrations of Pb treatment alone or in combination with SiO_2 NPs (the bars with the same colors), while the lowercase letters indicate statistically significant differences within each concentration of Pb treatment alone or in combination with SiO_2 NPs (the bars with different colors) according to Tukey's test ($p < 0.05$)

Table 4 The rate of increase in bamboo shoot and root biomass production under the various concentrations of Pb–(SiO_2 NPs) compared to their control treatments (Pb)

Concentration of (SiO_2 NPs) combination	50 µM		250 µM		500 µM		1000 µM		1500 µM	
	100 µM	500 µM	100 µM	500 µM	100 µM	500 µM	100 µM	500 µM	100 µM	500 µM
Shoot (fold)	1.08	1.13	1.14	1.26	1.21	1.41	1.02	1.14	1.04	1.13
Root (fold)	1.08	1.23	1.10	1.25	1.24	1.43	1.11	1.24	1.16	1.16

major mechanism controlling H_2O_2 concentration (Li and Jin 2007); it can scavenge ROS using the sulfhydryl group of GSH by reducing disulfide bonds in glutathione (Zitka et al. 2012). PAL plays an important role in the biosynthesis of lignins, phytoalexins, and phenolics (Ryals et al. 1996). PAL is an important indicator of plant stress (Leyva et al. 1995; Sanchez-Ballesta et al. 2000) and can be effective in determining abiotic (heavy metals, UV, and temperature) and biotic (viruses, bacteria, fungi) stresses, as demonstrated by increasing PAL accumulation in many phenolics in a variety of different experiments (Solecka and Kacperska 2003; Sgarbi et al. 2003). The results of our experiment indicated that antioxidant enzyme activities increased with the addition of SiO_2 NPs. Many researchers studying various plants have confirmed that silicon increases antioxidant enzyme activities. These different plants include rice (Song et al. 2011), barley (Gunes et al. 2007), cotton (Farooq et al. 2013), peanut (Shi et al. 2010), soybean (Miao et al. 2010), ramie (Tang et al. 2015), *Brassica chinensis* L. (Song et al. 2009), *A. thaliana* (Khandekar and Leisner 2011), and banana (Li et al. 2012). The efficiency of the effect of SiO_2 NPs on antioxidant activity is directly related to the specific concentration of heavy metals. Thus, with high levels of heavy metals, antioxidants may be unable to efficiently reduce the ROS caused by heavy metals (Adrees et al. 2015). This pattern occurred in our bamboo species; the greatest impact of SiO_2 NPs on antioxidants was in combination with a low level of Pb and, undoubtedly, the SiO_2 NPs could not help plants ameliorate Pb toxicity by stimulating antioxidant activities at high concentrations (or the effect was negligible). In general, the level of antioxidant activity under stressful conditions could be related to plant species, plant genotype (Hall 2002), the type of metal element, and growth conditions (Adrees et al. 2015).

Singlet oxygen (1O2) and hydrogen peroxide (H_2O_2) are two known nonradical ROS molecules that can increase with rising ROS levels due to heavy metal stress (Gill and Tuteja 2010; Sharma et al. 2012). In one experiment, the results showed that silicon can increase the activities of enzymes, including CAT, SOD, and APX in rice exposed to Zn and

reduce MDA and H_2O_2 (Song et al. 2011). This effect has also been reported in cucumbers exposed to Mn; silicon has the ability to reduce the lipid peroxidation caused by ROS such as H_2O_2 (Feng et al. 2009). Similar results were obtained in maize exposed to Mn (Zlatimira et al. 2008) and *Brassica chinensis* L. exposed to cadmium (Song et al. 2009). In other experiments on rice exposed to Zn, silicon could decrease H_2O_2 content and lipid peroxidation. Additionally, researchers concluded that the amelioration of Zn toxicity by silicon is related to increased antioxidant activity and membrane integrity. However, they mentioned the role of silicon in the reduction of Zn transport from the roots to the shoots (Song et al. 2011). The results obtained from the analysis of our bamboo species data indicated that SiO_2 NPs were able to control and scavenge ROS by reducing H_2O_2 levels. Additionally, it is clear that the high concentration of SiO_2 NPs (500 µM) had a significant impact. Silicon played an ameliorative role regarding plasma membrane and tonoplast functions, preserving the integrity of cellular structures, such as the stability of protein and lipids involved in cell membranes, leading to decreasing lipid peroxidation and soluble protein content in plants under ion stress (Gong et al. 2005). In our experiment, the results confirmed that SiO_2 NPs preserve cell membrane integrity by reducing the content of soluble proteins incorporated in the cell membrane, which is exposed to Pb stress. Additionally, different concentrations of SiO_2 NPs can have an essential role in reducing the soluble protein content, and the effect was larger with a high dose of SiO_2 NPs than with low concentrations of SiO_2 NPs. However, under high levels of Pb toxicity (1000 µM and 1500 µM), SiO_2 NPs did not have a considerable impact on the reduction of metal stress. The ameliorative effect of silicon on the increase in soluble proteins has been reported in many experiments, including in *maize* (Moussa 2006) and *Cnaphalocrocis medinalis* (Han et al. 2016). PPO and POD are two enzymes that are involved in several responses to cell damage (Michalak 2006; Ashry and Mohamed 2011). These enzymes are involved in oxidation processes and play an important role in catalyzing the formation of lignin and other oxidative phenols (Avdiushko et al. 1993). PPO has the ability to catalyze the oxidation of polyphenols and the hydroxylation of lignins and monophenols in plant cells (Trivedi et al. 2013; Hajiboland et al. 2017). PPO is one indicator of the oxidation process in plant cells. In the case of PPO, the results obtained by analyzing our data indicated that SiO_2 NPs reduce the oxidation of polyphenols in plant cells by decreasing the PPO activity in the plant under Pb stress. This happened in the 'latent form', and it can be concluded that the increase in PPO content activates and stimulates a 'latent phenolase' in plant cells (Aery and Mali 2012). This effect can preserve the integrity of plant cells, allowing them to cope with metal stress. However, at high concentrations of Pb (1000 µM and 1500 µM), this trend decreased. The reduction of PPO by silicon has been reported in some studies (Gomes et al. 2005; Ranger et al. 2009).

It appears that silicon, through a mechanism such as guiding light to the mesophyll tissue, increases the light absorption efficiency (Hattori et al. 2005). Increased chlorophyll content and chlorophyll fluorescence induced by silicon have been reported in sorghum under water deficit (Ma and Takahashi 2002), in wheat under drought stress (Maghsoudi et al. 2016) and metal stress conditions, and in *maize* under Zn stress (Kaya et al. 2009). The results obtained in one study on rice indicated that silicon can increase chlorophyll (a + b) content in the plant under Zn stress; the researchers mention that this improvement in chlorophyll content was related to an increase in the antioxidant activity caused by silicon, which can inhibit the transport of Zn from the root to the shoot. Additionally, they mention that silicon protects photosynthesis by upregulating the photochemical reaction, which is evidenced by increased chlorophyll fluorescence parameters (Song et al. 2014). Similar to the results obtained in rice plants under cadmium treatment with added silicon, these authors concluded that silicon can ameliorate toxicity associated with low concentrations of Cd by increasing light-use efficiency (Nwugo and Huerta 2008). The results obtained in our experiment indicated that SiO_2 NPs can lead to improved chlorophyll contents and carotenoids, resulting in higher total Chla + Chlb in bamboo under Pb stress. As a result, the considerable increase observed in the chlorophyll content of the SiO_2 NPs-treated bamboo plant under low levels of Pb was associated with enhanced photosynthetic activities. This finding is related to increased antioxidant enzyme activity at the low and middle concentrations of Pb in combination with SiO_2 NPs, which is consistent with the results obtained by Song et al. (2014). The results revealed that the application of SiO_2 NPs at 500 µM had a greater effect than at 100 µM on the increase in chlorophyll content and, eventually, photosynthesis metabolism in bamboo species under Pb stress.

Many studies have reported that silicon can increase biomass in plants under metal stress, including maize (*Zea mays* L.) under cadmium stress (Liang et al. 2005; da Cunha et al. 2008) and Zn stress (Da Cunha and Do Nascimento 2009), strawberry under cadmium stress (Treder and Cieslinski 2005), rice (*Oryza sativa L.*) seedlings under Zn (Gu et al. 2012) and arsenate (As) stress (Guo et al. 2005, 2007), and barley under AL stress (Liang et al. 2001). There are some important mechanisms of the silicon-induced improvement in biomass under heavy metal toxicity. One of the main mechanisms of silicon in the response to heavy metal stress is the reduction of metal uptake by plants and the reduction of silicon transport from roots to shoots (Sivanesan and Park 2014). In an experiment in wheat, silicon reduced the CD concentration in shoots and the CD uptake in roots, which led to an increase in plant biomass in shoots and roots

(Rizwan et al. 2012). Similar results have been reported in *Brassica chinensis* L. (Song et al. 2009), maize (Liang et al. 2005), and rice (Shi et al. 2005a, 2005b) under cadmium stress. In contrast, silicon can help elongate leaves in the basal zones through several mechanisms, including the following: (1) the enhancement of cell wall extensibility, which occurs in roots by strengthening endothermal cell walls; or (2) maintenance of the extensibility of young cell walls in mature and apical–basal regions (Taleahmad and Haddad 2011), which can help increase plant biomass under stressful conditions. The results obtained in our study indicated that SiO_2 NPs can increase biomass as measured by both dry and wet weight indexes, reversing the effect of Pb toxicity on plants. It seems that the increases in the antioxidant capacity and photosynthetic properties induced by SiO_2 NP application play important roles in increasing plant biomass and yield, with considerable positive effects at low and medium Pb levels in combination with SiO_2 NP application.

Conclusion

SiO_2 NPs may play an essential physiological role in improving plant growth and in the amelioration of toxicity of plants under Pb stress. However, SiO_2 NPs have a different effect in various plants and different levels of heavy metals. In the present study, we report that SiO_2 NPs increased plant growth in this bamboo species under Pb toxicity via mechanisms such as increasing antioxidant enzyme activities, reducing lipid peroxidation and protecting plant cells, which are related to scavenging ROS in cells with reduced H_2O_2 content. In the current experiment, SiO_2 NPs improved photosynthetic efficiency and increased plant biomass, which were related to increased antioxidant activity in plants under Pb stress. It can be concluded that SiO_2 NPs at a concentration of 500 μM have a significant effect on plant growth under Pb toxicity. Additionally, the results showed that SiO_2 NPs had considerable detoxification effects at 250 μM and 500 μM Pb. We conclude that the efficiency of SiO_2 NPs depends on the heavy metal concentration, as we observed in our experiment, and that the effect of SiO_2 NPs at high concentrations of Pb (1000 μM and 1500 μM) is negligible. Therefore, we consider that the optimal level of SiO_2 NPs as the main contributing factor to improving plant growth and ameliorating Pb toxicity in the present experiment.

Author contribution statement AE conceived the research, performed the investigation, and composed the initial draft of the manuscript. YD provided support, advice, and guidance throughout the experiment. FM contributed to the revision of the manuscript and also provided insights into different aspects of the work. YX aided with the statistical analysis. XZ and YW assisted in laboratory experiments.

Acknowledgements This work was supported by Nanjing Firestry University (Start-Up Fund) and Bamboo Research Institute for the current study. Special Fund for this work was Supported by National Key Research & Development program of China (Integration and Demonstration of Value & Efficiency—increased Technology across the Industry Chain for Bamboo, 2016 YFD0600901).

Compliance with ethical standards

Conflict of interest The authors declare that there is no conflict of interests regarding the publication of this paper.

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