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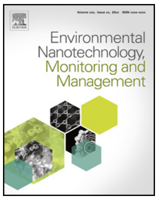

Effects of silicon on growth, root anatomy, radial oxygen loss (ROL) and Fe/Mn plaque of *Aegiceras corniculatum* (L.) Blanco seedlings exposed to cadmium

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ABSTRACT

Biomass, root anatomy, the location of Cd, radial oxygen loss (ROL) and Fe/Mn plaque in *Aegiceras corniculatum* (L.) blanco were investigated under Si and Cd treatments. The results revealed that Si alleviated the inhibition of growth due to Cd stress. Furthermore, Si prompted the development of apoplastic barriers in roots under Cd stress. Promotion of the apoplastic barrier caused the reduction of ROL. The effect of Si on the formation of Fe/Mn plaque was contrary, but Si reduced the content of Fe plaque and increased the content of Mn plaque. However, the content of Cd on Fe/Mn plaque was significantly increased by Si, which could possibly block the absorption of Cd in the root from the growth media. The present study proposed new evidence of adaptive strategy on metal tolerance and the effect of Si on metal tolerance by *A. corniculatum* seedlings.

1. Introduction

Mangrove ecosystems are distributed in tropical and subtropical coastal regions, where they play a key role in the ecological balance of estuaries and seashores. However, it has been reported that more metallic contaminants have been input into mangrove forests with the development of economies and populations. Research into response and tolerance mechanisms with respect to heavy metal in mangroves has been a major topic in the past three decades. Some research studies have suggested that the rhizosphere processes of mangrove plants can affect the bioavailability and mobility of heavy metals while limiting heavy-metal uptake (Lu et al., 2007; Zhou et al., 2011; Xie et al., 2012; Cheng et al., 2012a,b). For example, the radial oxygen loss (ROL) of the root induces Fe/Mn plaque formation on the root surface of mangrove (Pi et al., 2010). The Fe/Mn plaque can alter the forms of heavy metals in the rhizosphere through a series of physical and chemical process, which affect heavy-metal transfer. The root of mangrove can excrete low molecular weight organic acid, which plays a key role in reducing the input of heavy metals in mangrove plants (Xie et al., 2012).

Silicon is not listed among the higher plant essential elements, but the direct and indirect beneficial effects of Si on plant growth and development are well known. Many studies have reported that Si may be involved in metabolic or physiological and/or structural activity in higher plants that are exposed to abiotic and biotic stresses (Liang et al., 2003; Shen et al., 2010). It has been reported that Si increases some plant species' tolerance to toxic metals such as manganese (Mn), aluminum (Al), cadmium (Cd), zinc (Zn) and arsenic (As) (Liang et al., 2007). The strategies of silicon-mediated alleviation to heavy-metal stress vary with plant species. Some studies have suggested that Si decreases heavy-metal intake through an external or internal mechanism and alleviates the toxicity (Kidd et al., 2001; Shi et al., 2010; Zhang et al., 2013). In some plants, Si treatment can alter the sub-cellular distribution of heavy metals and increase the binding of heavy metals to the cell walls, thereby decreasing the heavy metals' toxicity to the cell (Ye et al., 2012; Zhang et al., 2014; Shi et al., 2010). Some studies have found that Si stimulated antioxidant systems and reduced membrane lipid peroxidation under heavy-metal stress (Shi et al., 2005, 2010).

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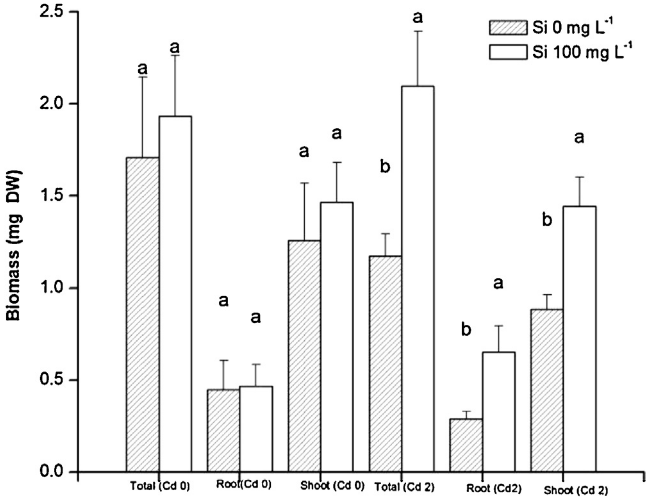

Fig. 1. Biomass of *A. corniculatum* seedlings after eight weeks of cultivation.
Note: Cd 0 and Cd 2 mean the concentration of Cd in the Hoagland's solution was 0 mg L^{-1} and 2 mg L^{-1}, respectively. Si 0 and Si 100 mean the concentration of Si in the Hoagland's solution was 0 mg L^{-1} and 100 mg L^{-1}, respectively.

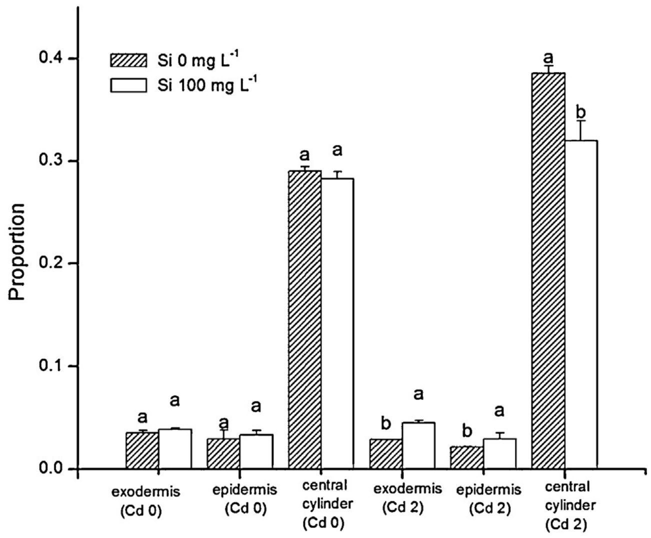

Fig. 2. The ratio of the cross-sectional width of epidermis, exodermis and central cylinder to the root diameter in root 1 cm section along lateral roots of *A. corniculatum* (%).
Note: Exodermis – the ratio of the cross-sectional width of the exodermis to the root diameter; epidermis – the ratio of the cross-sectional width of the epidermis to the root diameter; central cylinder – the ratio of the cross-sectional width of the central cylinder to the root diameter; values are means (%) ±SD ($n = 3$). Different letters mean significant differences between the treatments at 0.05 level.

It is thought that there are high concentrations of available Si in mangrove wetlands due to sediments, which are composed of fine particles with high organic matter content but low pH and are periodically agitated by tides (Peters et al., 1997; Marchand et al., 2004; Qin and Weng, 2006; Ye et al., 2012). The effect of Si on mangrove has been studied recently. Ye et al. (2012) and Zhang et al. (2014) investigated the amelioration by Si of Cd stress of *Kandelia obovata* (S., L.) Yong and *Avicennia marian*, respectively. They suggested Si enhanced the binding of Cd to the cell walls in the root tips and restricted its apoplastic transport in *K. obovata* (S., L.) *Yong* and *A. marian*, thus playing an important role in the amelioration of Cd toxicity. Zhang et al. (2013) found that the amelioration by Si of Cd toxicity was related to the alteration of the anatomy of the roots and the increased ROL of *A. marian* seedlings. *Aegiceras corniculatum* is also an important mangrove plant species in southeastern China. The effect of Si on *A. corniculatum* has not yet been reported. The aim here was to investigate whether Si ameliorates the toxic effects of Cd and whether the effect of Si is correlated with the alteration of root-anatomy structure and ROL.

2. Materials and methods

2.1. Plant culture and experimental treatments

Healthy propagules of *A. corniculatum* were planted in vermiculite in the greenhouse, with average day/night temperature of 25 °C/20 °C and average relative humidity of 75%. After three months of growing, the uniform seedlings were transplanted to plastic buckets containing 1.5 L Hoagland's solution, which was prepared using distilled water. After two weeks of hydroponics, two levels of Cd (control and 2 mg L^{-1}) and two levels of Si (control and 100 mg L^{-1}) were developed, being $CdCl_2$ and Na_2SiO_3, respectively. A completely randomized design was applied. Each treatment had three replicates, and the solution was changed every three days. The initial pH of nutrient solutions was adjusted to 6.5 by adding 0.1 M HCl or 0.1 M NaOH. Seedlings were harvested after eight weeks of growth.

2.2. Measurements of plant biomass

The seedlings were rinsed thoroughly with distilled water and divided into the roots and shoots. The plant materials were oven-dried for 15 min at 105, then at 70 until constant weight. Data was recorded in regard to the dry weights of the shoots and roots.

2.3. Observation of root anatomy

The anatomical structures of the healthy roots of different treatments were studied using fresh sections of different distances behind the root tip (0.8–1.0, 3.8–4.0 cm from the tip). Fresh root sections were collected and immediately fixed in FAA (formalin–acetic acid–alcohol) at 4 °C for 48 h. Samples were dehydrated in a graduated solution series of TBA (*tert*-butyl alcohol) and were then embedded in paraffin. Root sections with a thickness of 10 μm were obtained using the RM2125RT rotary microtome. Berberine-aniline blue staining was used to observe the root anatomy and detect Casparian bands using the method described by Brundrett et al. (1988). Specimens were analyzed using a fluorescence microscope (Olympus IX81, Japan) and light micrographs were acquired by a digital camera (Olympus DP-50, Japan). The images were analyzed for the thickness of the epidermis, exodermis, endodermis and Casparian band, as well as the cross-sectional area of the xylem and the central cylinder using the Image-Pro Plus 6.0 analysis software.

2.4. The localization of Cd

Dithizone was used to locate Cd, based on the ability of dithizone in producing a reddish color compound after reacting with cadmium (da Cunha and do Nascimento, 2009; Seregin and Ivanov, 1997). The location of Cd in the sections of the root tips was observed, and photos were taken immediately after they were dyed in a solution of dithizone (30 mg dipheniltiocarbazone dissolved in 60 mL of acetone and 20 mL of distilled water) for about 2 h.

2.5. Measurement of radial oxygen loss (ROL) from entire roots

ROL from entire roots was analyzed with titanium(III) citrate buffer calorimetrically. Each of the entire roots was inserted into a beaker with the nutrient solution purged with N_2 gas for 1200 s. The layer of paraffin oil about 20 mm thick covered the solution