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REVIEW

Effects of calcium at toxic concentrations of cadmium in plants

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Abstract

Main conclusion **This review provides new insight that calcium plays important roles in plant growth, heavy metal accumulation and translocation, photosynthesis, oxidative damage and signal transduction under cadmium stress.**

Increasing heavy metal pollution problems have raised word-wide concerns. Cadmium (Cd), being a highly toxic metal, poses potential risks both to ecosystems and human health. Compared with conventional technologies, phytoremediation, being cost-efficient, highly stable and environment-friendly, is believed to be a promising green technology for Cd decontamination. However, Cd can be easily taken up by plants and may cause severe phytotoxicity to plants, thus limiting the efficiency of phytoremediation. Various researches are being done to investigate the effects of exogenous substances on the mitigation of Cd toxicity to plants. Calcium (Ca) is an essential plant macronutrient that involved in various plant physiological processes, such as plant growth and development, cell division, cytoplasmic streaming, photosynthesis and intracellular signaling transduction. Due to the chemical similarity between Ca and Cd, Ca may mediate Cd-induced physiological or metabolic changes in plants. Recent studies have shown that Ca could be used as an exogenous substance to protect plants against Cd stress by the alleviation of growth inhibition, regulation of metal uptake and translocation, improvement of photosynthesis, mitigation of oxidative damages and the control of signal transduction in the plants. The effects of Ca on toxic concentrations of Cd in plants are reviewed. This review also provides new insight that plants with enhanced Ca level have improved resistance to Cd stress.

Keywords Metal accumulation · Oxidative stress · Photosynthesis · Signal transduction

Introduction

Heavy metals are derived from natural sources and anthropogenic activities. Heavy metal pollution has attracted widespread attentions in recent years due to the overexploitation and the abuse of the toxic heavy metals (Huang et al. 2008; Islam et al. 2015; Sakan et al. 2015; Yang et al. 2015b). Compared with other pollutants, heavy metals usually cannot be degraded and are easy to be bioaccumulated through the food chain, thus posing long-term threat to both the ecosystems and human health (Huang et al. 2015; Jarup 2003). Among all the heavy metals, cadmium (Cd) is a non-essential and highly toxic heavy metal. It is mainly derived from anthropogenic activities, such as mining, electroplating, metallurgy, waste combustion and the abuse of Cd-containing pesticides and fertilizers (Cheng et al. 2014; Fagerberg et al. 2015). In addition, Cd is classified as a probable human carcinogen, which may cause cardiovascular disease, skeletal damage, and lung, prostate and kidney cancer in human bodies (Hong and Yan 2015; Brodziak-Dopierała et al. 2015;

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Yang et al. 2015a; Ansari et al. 2015). Therefore, measures should be taken to deal with the problems of Cd contamination.

Remediation of Cd-contaminated soils can be carried out by physical, chemical and biological technologies (Huang et al. 2016; Singh and Prasad 2014). Compared with conventional soil remediation practices, phytoremediation has been considered as a developing and promising alternative technology owing to its cost-efficient, high stability, and environment-friendly properties (Shahid et al. 2014; Koptsik 2014; Ali et al. 2013). The species such as *Leonotis leonurus, Eucalyptus globulus, Helianthus annuus* L. and *Athyrium wardii* showed high Cd accumulation ability, which indicated that using phytoremediation for Cd-contaminated soil remediation is feasible (Buhlungu and Ntoni 2002; Luo et al. 2015; Kastori et al. 1992; Zhang et al. 2014a). However, high Cd accumulation will result in metal-induced toxic symptoms of the plants (Tran and Popova 2013; Li et al. 2016). It has been reported that Cd could alter the synthesis of RNA, cause leaf roll and chlorosis, reduce photosynthesis rate, inhibit stomata opening and decrease the activities of several enzymes in plants (Kesseler and Brand 1995; Salt et al. 1995; Gallego et al. 1996; Obata and Umebayashi 1997). Plants have evolved various mechanisms to cope with Cd stress, such as cell wall binding, metal chelation with proteins and the compartmentation of Cd in the vacuole. Nevertheless, the uptake of Cd was inefficient and the toxic effects of Cd were pronounced especially with high Cd accumulation in most plant species. To develop phytoremediation technologies, significant progress in improving Cd-remediation capability of plants has been made in the last few years through comparative physiological, cytological and genomic studies (Bhargava et al. 2012). The addition of exogenous substance has been recognized as a feasible technique to improve the phytoremediation efficiency of heavy metals contaminated soil. For example, the application of the exogenous nitric oxide, citric, oxalic acid, selenium and silicon has been found to prevent the growth inhibition, mitigate the oxidative stress and ameliorate other deleterious effects of Cd in *Boehmeria nivea* (L.) Gaud (Wang et al. 2015; Li et al. 2014; Wang et al. 2014; Tang et al. 2015). Meanwhile, the study conducted by López demonstrated that plants could increase their metal accumulation potential by using ethylenediaminetetraacetic acid, gibberellic acid, kinetin and indole-3-acetic acid, thus increasing the phytoremediation efficiency (López et al. 2005, 2007). Specifically, it has been reported that exogenously applied calcium (Ca) could alleviate the toxicity of Cd in *Arabidopsis* seedlings, *Gamblea innovans*, tobacco and *Maize* seedlings (Choi and Harada 2005; Hayakawa et al. 2011; El-Enany 1995; Suzuki 2005). Ca, a divalent cation, has high physical resemblance to Cd and it may regulate Cd-induced physiological or metabolic changes in the organisms (Kinraid 1998; Dayod et al. 2010). Ca is recognized as a central regulator for plant biochemical and physiological processes (Hirschi 2004) and this may involve the alleviation of heavy metal-induced toxicity to plants. Several recent investigations have demonstrated the important roles of Ca in plants resistance to Cd stress (Table 1). Ca was found to protect plants against Cd stress and the possible mechanisms are as follows: First, the alleviation of growth inhibition and the regulation of Cd accumulation and translocation are the superficial phenomenon of Ca protection; Additionally, Ca alleviates Cd-induced oxidative stress in plants by scavenging reactive oxygen species (ROS), increasing antioxidant levels and enhancing antioxidant enzymes activities; Furthermore, the detoxification of Cd in plants might also involve the enhancement of plant photosynthesis and the crucial roles of Ca in Ca-dependent signaling transduction under Cd stress. In this review, the current knowledge of the effects of Ca at toxic concentrations of Cd in plants was summarized, and the focus is to review the effects of Ca on plant growth, metal accumulation, oxidative stress, photosynthesis, and Ca-dependent signal transduction in plants under Cd stress (Fig. 1).

Effects of exogenous Ca on plant growth under Cd stress

Growth inhibition is one of the distinct symptoms of metal toxicity. It has been reported that Cd could induce growth inhibition and reduce the biomass production of plants in most species (Deng et al. 2014; Dias et al. 2012). A reduction in root growth is the most distinct physiological response of plants to heavy metal stress since roots are in direct contact with contaminants. As found by Stravinskienė and Račaitė (2014), the effect of Cd on root lengths reduction of *Trifolium repens* L. was more remarkable than that of shoots. Furthermore, the negative impacts of Cd on plant growth varied with different plant species and were in a concentration-dependent manner. Four concentrations of Cd (50, 100, 200, 400 μM) were used to investigate the effects of Cd on plant growth of *Atriplex halimus* subsp. *schweinfurthii* (Nedjimi and Daoud 2009). Results demonstrated that Cd-treated seedlings showed significantly reduced fresh and dry weights of the shoots and roots, and the biomass production was markedly decreased with increasing Cd concentrations.

Ca is an essential element for plant growth and development. It has been concluded that Ca could positively affect plant height, root length and the biomass production of the plants under Cd stress. One of the possible reasons is represented by the involvement of Ca in plant cell division. For example, supplementation of the medium with Ca was

Table 1 Roles of Ca in the alleviation of the deleterious effects of Cd in plants

Plant species	Cd content	Ca content	Effects of exogenous Ca	References
Brassica juncea L.	1.79 or 2.68 mM	50 mM	Improved growth and biomass yield; Enhanced oil and proline contents; Decreased Cd conten and MDA levels; Promoted SOD, APX, GR activities	Ahmad et al. (2015)
Matricaria chamomilla L.	120 or 180 µM	0.1, 1, or 5 mM	Reduced Cd content and ROS accumulation; Increased proteins contents and dry weight; Decreased SOD, POD, CAT activities and MDA content	Farzadfar et al. (2013)
Lens culinaris Medic.	10, 20 or 40 µM	5 mM	Decreased Cd accumulation; declined H_2O_2 and MDA levels, enhanced fresh weight; modulated SOD, APX, CAT, DHAR and GR activities	Talukdar (2012)
Sedum alfredii H.	400 µM	6 mM	Decreased Cd content, ROS and MDA levels; alleviated growth inhibition; altered CAT, SOD, POD activities and non-protein thiols contents; elevated GSH content	Tian et al. (2011)
Rice	100 µM	1, 5, or 10 mM	Alleviated growth inhibition; elevated NO, pectin and hemicellulose contents; decreased Cd, protein thiols, and non-protein thiols levels	Zhang et al. (2012)
Wedelia trilobata L.	100, or 300 µM	10, 20 or 30 mM	Enhanced mitotic index; decreased chromosomal aberration rate	Shi et al. (2014)
Vicia faba L.	200 µM	40 mM	Improved growth traits and Ca, potassium, chlorophyll *a*, *b*, and proline content; Increased CAT, POD and SOD activities; Reduced Cd content and MDA levels	Siddiqui et al. (2012)
Micrasterias	150 µM	232 µM or 2 mM	Prevented chloroplast structure disturbance; Improved photosynthesis efficiency; Reduced autophagy induction	Andosch et al. (2012)
Pisum sativum L.	25 or 50 µM	1 or 5 mM	Increased CAT, POD activities; elevated ascorbic acid, tocopherol and carotenoids contents; changed α-esterase, β-esterase and acid phosphatase isozymes concentrations; Improved soluble protein and carbohydrate contents; decreased phenol, proline and MDA levels	El-Beltagi and Mohamed (2013)
Brassica napus L.	500 µM	2 mM	Reduced intercellular CO_2 level, non-photochemical quenching and Cd accumulation; alleviated growth inhibition; improved photosynthetic rate, stomatal conductivity and transpiration rate	Wan et al. (2011)

found to ameliorate a wide variety of Cd-induced mitotic abnormalities in the organisms. The application of Ca alleviated Cd-induced growth reduction by decreasing the frequency of chromosomal aberration and increasing the mitotic index in *Vicia faba* plants (Mohamed 2012). Besides, the interactions between Ca and plant growth regulators, such as gibberellic acid, auxin and ethylene, might also alleviate plant growth inhibition under Cd stress. As found by Brunetti et al. (2011), Cd treatments significantly suppressed the root growth of *Arabidopsis* seedlings. Li et al. (2015a) further studied the impacts of Ca on Cd toxicity to *Arabidopsis* seedlings. They found that Ca supplementation restored normal auxin transportation and distribution in the plants, and, thereby, mitigated Cd-induced plant growth depression. Furthermore, the addition of exogenous Ca contributes to an enhancement of the essential mineral elements uptake and these elements are beneficial to plant growth and development. For instance, 0.1 mM Cd treatments significantly reduced the root, mesocotyl and coleoptile lengths of maize seedlings. The application of 10 mM Ca counteracted the deleterious effect of Cd on maize growth by the maintenance of high levels of potassium (K) and sodium (Na) (Kurtyka et al. 2008). Similarly, the suppressed contents of total phenol, flavonoid and mineral elements in Cd stress plants were restored with the addition of exogenous Ca, thus improving the crop yield of *Cicer arietinum* L. (Parvaiz et al. 2016).

Effects of exogenous Ca on Cd accumulation and translocation

Although Cd is a non-essential element, the uptake and translocation of Cd in plants are quite common (Zhang et al. 2014b). The plants, such as *Phragmites australis*, *Pentas lanceolata* and *Bechmeria nivea* L. Gaud, exhibited a relatively high capability of Cd accumulation (Iannelli et al. 2002; Chang et al. 2013; Liu et al. 2007). However, there are no confirmed specific transport channels for Cd uptake in plants so far to our knowledge. Non-essential metals could be absorbed by plants via the transporters and channels for essential elements (Rodriguez-Hernandez et al. 2015; Mleczek et al. 2012). For example, IRT1 gene is a major transporter responsible for iron uptake in *Arabidopsis*. The over expression of IRT1 resulted in a higher level of Cd accumulation, suggesting that uptake

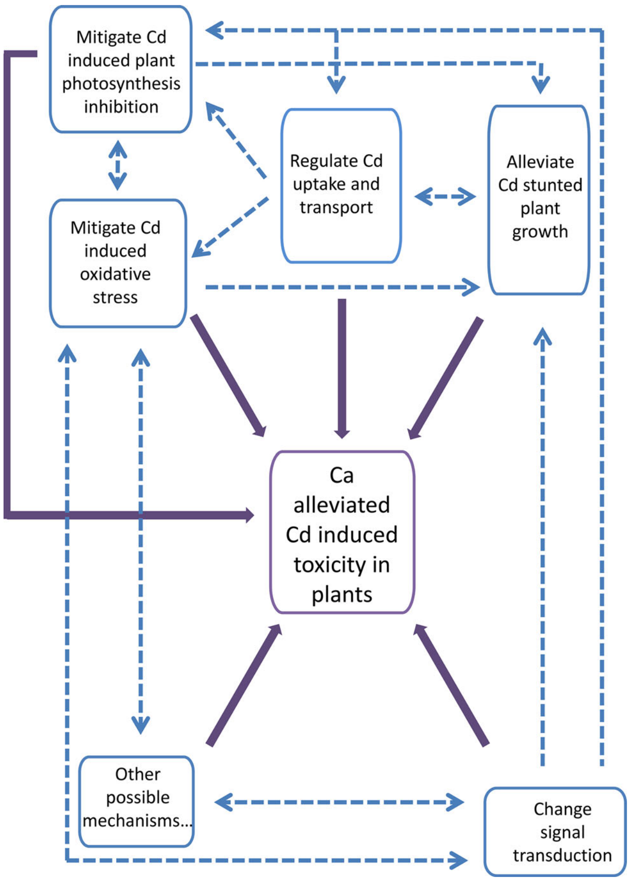

Fig. 1 Possible mechanisms of the protective role of Ca against Cd-induced toxicity in plants

transporter of essential elements could provide an effective means of metal absorption in the plants (Connolly et al. 2002). Similarly, it has also been found that Cd could be taken up by rice through manganese transporters (Sasaki and Ma 2012). Specifically, the study conducted by Perfus-Barbeoch et al. (2002) found that Ca channels were permeable to Cd and Cd could enter plant guard cell through Ca channels. Inversely, it also has been suggested that essential elements might impact the uptake and transport of non-essential metals in plants. Therefore, Ca will affect Cd accumulation and translocation in plants and the influences are complex and varied in different plant species. In runner bean, 255 mg/L Ca and Cd treatment plants showed a remarkably higher Cd accumulation specificity than the only Cd treatment group (Skórzyńska-Polit et al. 1998). Low concentration of Ca treatment also enhanced the uptake of Cd in the roots of *Brassica juncea* and *Sesbania sesban* (Eller and Brix 2016). On the other hand, the application of exogenous Ca significantly reduced the uptake of Cd in most of the plants species (Suzuki 2005; Kurtyka et al. 2008). Significant reduction of Cd concentrations in rice roots were observed with the addition of 100 μM Ca, suggesting that the protective effects of Ca on Cd toxicity could be predominantly related to its inhibition of Cd absorption in the roots (Kim et al. 2002). Similar decreases of Cd accumulation were observed in soybean and wheat roots in the presence of 1 and 10 mM Ca (Yang and Juang 2015). In addition, the effects of Ca on Cd accumulation varied in different plant organs. As found by Hayakawa et al. (2011), Cd concentrations in the roots were increased in Ca + Cd treatment plants when compared with the only Cd treatment plants, but Ca treatment negatively affected the uptake of Cd in *G. innovans* stems and leaves.

It is generally accepted that plant roots possess a much greater ability for Cd accumulation than the aerial parts. Apart from the absorption capability, phytoremediation efficiency also depends on the translocation ability of the pollutants in plants. One of the indicators used to estimate the transportation of Cd in the plants is the translocation factor (TF), which is defined as the ratio of metal contents in the aboveground parts to that in the roots (Ajm and Whiting 2002; Kováčik 2013; Jiali et al. 2013). Ca is found to play a crucial role in heavy metal transport from plants roots to shoots. It has been reported that the treatment of Ca with 120 μM Cd could increase the TF value of Cd in chamomile plants, indicating that Ca could promote Cd translocation from plant roots to the aboveground parts (Farzadfar et al. 2013). Since Cd retained in the roots can be released back into the environment, the increased TF value of Cd induced by the addition of exogenous Ca is beneficial to the phytoremediation of Cd-contaminated soil.

The influences of Ca on Cd uptake and transport can be attributed mainly to the competition between Ca and Cd. Ca, as a divalent cation, shares many transporters, transport-channels and binding sites with Cd, and, thereby, facilitated or suppressed Cd accumulation and translocation in the plants (Rodriguez-Hernandez et al. 2015). A gene encoding Ca transporter proteins was isolated from *Sedum alfredii*, and the over-expression of this gene enhanced Cd accumulation in tobacco (Zhang et al. 2015). Moreover, the impacts of Ca on Cd accumulation and translocation are dose-dependent (Marchetti 2013). In our previous study, we found that the application of 5 mM Ca significantly reduced Cd accumulation in *B. nivea* (L.) Gaudich. Instead, under the treatment of 1 mM Ca, the enhancement of Cd uptake and the promotion of Cd translocation were observed (Gong et al. 2016). In addition, the role of Ca in the protection of plasma membrane also will influence the effects of Ca on Cd accumulation. Plant plasma membrane acts as a barrier of Cd into plant cells. It has been noted that Ca plays a key role in the control of the stability and integrity of the cell membrane (Jones and Lunt 1967), thus impeding the entrance of Cd into plant cells. On the other hand, the negative charged membrane potential which provides a driving force for metal adsorption was thought to be changed by the addition of exogenous Ca. A study conducted by Kinraid (1998) demonstrated that high level of Ca treatment reduced Cd accumulation by decreasing the cell-surface negativity of plant cell membranes (Kinraid 1998).

Alleviation of Cd-induced oxidative stress

ROS are continuously produced in the plants as byproducts of aerobic metabolism processes, such as respiration and photosynthesis (Apel and Hirt 2004; Lehmann et al. 2015; Saed-Moucheshi et al. 2014). The generated ROS, acting as signaling molecules, control various processes including pathogen defense, programmed cell death and stomata behavior in the plants (Kärkönen and Kuchitsu 2015). However, the excess amount of ROS could react with a large variety of biomolecules, thus leading to tissue necrosis and may ultimately kill the plants (Apel and Hirt 2004). Under physiological steady state, the production and scavenging of ROS is in equilibrium in the plants. Nevertheless, environmental factors, such as salt, light, drought and heavy metals stress, will break the equilibrium between ROS generation and scavenging. A number of researchers have noted that Cd-induced deleterious effect in the organisms could be ascribed to, at least partially, the oxidative burst due to the excessive production of ROS.

Large amounts of ROS including superoxide radicals ($O_2^{\cdot -}$), hydrogen peroxide (H_2O_2) and hydroxyl radical ($O\dot{H}$) are produced under Cd stress and thereby induce oxidative damages to plants (Perez-Chaca et al. 2014; Liu et al. 2015; Piterková et al. 2015; Xu et al. 2015). Ca has been implicated in the control of ROS production and scavenging of some plants (Srivastava et al. 2015). In *lentil* seedlings, Cd treatment presented an upward trend of H_2O_2 in plants shoots and roots, while the addition of Ca notably reduced the H_2O_2 levels of the Cd-treated seedlings (Talukdar 2012). It has also been demonstrated that Cd treatment considerably increased $O_2^{\cdot -}$ and H_2O_2 contents in chamomile, and the application of $CaCl_2$ significantly decreased the concentrations of the above two ROS in chamomile roots and the aboveground parts (Farzadfar et al. 2013). Furthermore, Tian et al. (2011) used fluorescence imaging to visualize the ROS production in plants directly. This study employed specific $O_2^{\cdot -}$ and H_2O_2 probes to better illustrate their generations. Results showed that the production of large amounts of $O_2^{\cdot -}$ and H_2O_2 were observed in *S. alfredii* roots under Cd treatment. The application of exogenous Ca resulted in a relatively slight fluorescence of these two substances, indicating low levels of ROS generation. It can be concluded that the controlled and regulated production of ROS is one of the Ca protective mechanisms against Cd-induced oxidative damages.

Plants have evolved sophisticated strategies containing enzymatic and non-enzymatic mechanisms to maintain ROS homeostasis under environmental stress (Mittler 2002). Anti-oxidative enzymes play major roles in enzymatic reactions of oxidation-resisting mechanisms. Superoxide dismutase (SOD) acted as the first line of defense against ROS, which catalyzed $O_2^{\cdot -}$ to H_2O_2. The overproduced H_2O_2 was then converted into H_2O by peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), etc. (Kumar et al. 2010; Cao et al. 2015). Ca is capable in the regulation of the activities of some enzymes related to ROS scavenging, which further strengthen plants capability to withstand the oxidative stress caused by Cd. Ahmad et al. (2015) studied the effects of Ca on the alleviation of Cd toxicity in *B. juncea* L. The researchers found that the application of Ca decreased Cd uptake, enhanced oil and proline contents, prevented growth inhibition, and promoted SOD, APX and GR activities in the plants. These results suggested that the enhanced antioxidant enzymes activities caused by Ca played a crucial role in the alleviation of Cd toxicity. Similarly, the addition of Ca to the culture media considerably mitigated Cd-induced oxidative stress by regulating the activities of SOD, APX, CAT, dehydroascorbate reductase (DHAR) and glutathione reductase (GR) in the shoots and roots of *Lens culinaris* Medic. seedlings (Talukdar 2012). In addition, it is noteworthy that Ca deficiency aggravated Cd toxicity in rice seedlings by negatively influencing the activities of APX, SOD, CAT and GR, which further certified the important roles of Ca in the anti-oxidative defense systems (Cho et al. 2012). Furthermore, Ca was found to regulate NADPH oxidases activity of plasma membranes under Cd stress, and these enzymes are responsible for ROS production in the plants (Heyno et al. 2008). The non-enzymatic antioxidant system is composed of a wide variety of non-enzymatic antioxidants, which provide protection to plants organelles and biomolecules by directly scavenging the overproduced ROS. The contents of antioxidants in plants tissues could be modified by the addition of exogenous Ca. In *Pisum sativum* L. seedlings, $CaCl_2$ was highly effective against Cd-induced oxidative burst by increasing the concentrations of antioxidants such as ascorbic acid (ASA), tocopherol and carotenoids (El-Beltagi and Mohamed 2013). Glutathione (GSH), an important antioxidant, plays a pivotal role in plant ascorbate–glutathione cycle and glutathione-peroxidase cycle (Xu et al. 2014). Tian et al. (2011) found that *S. alfredii* roots treated with Ca resulted in the decrease of Cd accumulation and H_2O_2 contents, as well as the increase of GSH level, suggesting that the alleviation effect of Ca against Cd-induced oxidative stress is related to the promotion of GSH biosynthesis. Besides, GSH is a precursor of phytochelatin (PCs) and PCs could chelate with Cd to form a stable Cd-contained substance for metal sequestration (Chao et al. 2011). A study using citrus plants demonstrated that the optimum content of GSH maintained by the addition of Ca improved plants resistance to Cd stress by increasing PC biosynthesis (Lopez-Climent et al. 2013). In addition, the excessive production of ROS in the plans may perturb the cellular redox homeostasis. In Cd-treated rice seedlings, the increase ratios of GSSG/GSH and DHA/ASA were found, indicating a gradual shift to the oxidized cellular redox status in the plants. Ca treatment significantly reduced GSSG/GSH and DHA/ASA ratios, suggesting that Ca-mediated pathways on the mitigation of Cd toxicity were associated with the maintenance of the cellular redox homeostasis in the plants (Srivastava et al. 2015; Rahman et al. 2016). Besides, a positive correlation between the expression of Ca transporter *CAX1* and Cd tolerance was observed in *Arabidopsis halleri* (Baliardini et al. 2015). As found by Baliardini et al., function loss of the Ca transporter *CAX1* led to higher ROS accumulation in the plants after Cd treatment, showing that Ca transporters were involved in the alleviation of plant oxidative damage under Cd stress.

The cellular oxidative damage in the plants has often been monitored by measuring lipid peroxidation (Spirlandeli et al. 2014). In *V. faba* L., exogenous Ca addition attenuated Cd-induced lipid peroxidation (Siddiqui et al. 2012). The alleviation of lipid peroxidation may be the result of the protective role of Ca in the control of the integrity and stability of the membranes structure and functions. The decrease of lipid peroxidation induced by the application of Ca under Cd stress has also been found in *L. culinaris* Medic., *P. sativum* L. and *Matricaria chamomilla* L. (Talukdar 2012; El-Beltagi and Mohamed 2013; Farzadfar et al. 2013).

Regulation of plant photosynthesis by Ca under Cd stress

Photosynthesis is the process in which plants utilize the energy of sunlight in the presence of chlorophyll. One of the deleterious effects caused by Cd is the inhibition of plant photosynthesis (Degl'Innocenti et al. 2014; Li et al. 2015b). It has been found that 10 and 50 µM Cd treatment could depress the maximum photochemical efficiency of photosystem II (PSII) and the net CO_2 assimilation rate in lettuce (Dias et al. 2012). In *Ceratopteris pteridoides*, the application of Cd negatively affected the photosynthesis of plants by decreasing the chlorophyll content and reducing the relative electron transport rate (Deng et al. 2014).

Ca plays important roles in the regulation of plant photosynthesis, including photosynthetic electron flow and the light-dependent metabolism reactions (Brand and Becker 1984; Hochmal et al. 2015). Ca is also required as the obligatory activators of H_2O oxidation in PSII (Miqyass et al. 2007). Ramalho et al. (1994) investigated the effects of Ca deficiency on *Coffea arabica* photosynthesis, which confirmed that Ca played a pivotal role in the maintenance of photochemical efficiency of PSII and in the stabilization of chlorophyll. Application of Ca to the growth media has been found to restore the photosynthesis efficiency in the plants under Cd stress. The pre-treatment of Ca ameliorated the decline of oxygen production and the structural damage of chloroplast caused by Cd in *Micrasterias*, and, therefore, rehabilitated the photosynthetic activity in the plants (Andosch et al. 2012). Furthermore, Ca is an essential cofactor of the catalytic inorganic core ($Mn_4CaO_xCl_y$) in PSII. Cd adversely affected the PSII via the substitution of Ca by Cd during the core assembly (Faller et al. 2005). Thus, applying appropriate concentrations of Ca could restore plant photosynthesis inhibited by Cd (Bartlett et al. 2008). However, the regulation of plant photosynthesis by Ca under Cd stress varied with different Ca concentrations. An excess content of Ca application was found to disturb the Pi level presented in chloroplasts, which aggravated the harmful effects of Cd on plant photosynthesis (Skórzyńska-Polit et al. 1998).

Ca-dependent signal transduction under Cd stress

Ca has been proposed to act as an intracellular “second messenger” that can transduce signals received by plant cells and mediate plant responses to the biotic and abiotic stresses such as pathogen invasion, salt, heat, light, drought and heavy metal stress (Dayod et al. 2010). Ca signatures are generated by the transient or sustained elevation of the cytosolic Ca content. The changed cytosolic Ca content will be perceived by Ca sensor proteins and then evoke downstream signaling responses (Huda et al. 2013; Lecourieux et al. 2006). Recent works have identified and characterized the following most common Ca sensors: Ca-dependent protein kinase (CDPK), calmodulin protein (CaM), calmodulin-like protein (CML), calcineurin B-like protein (CBL) and CBL-interacting protein kinases (CIPKs). The above Ca sensors translate Ca signatures through the modification of specific target proteins or genes expression (Hashimoto and Kudla 2011). The regulation of target proteins and protein related-genes expression play critical roles in the physiological processes of plants under environmental stress. The expression of heat-shock proteins and cold-responsive gene were regulated by CaM which imparted plant with thermo tolerance and freezing tolerance (Zhang et al. 2009; Stockinger et al. 2007). Besides, some members of the Ca sensors have been found to enhance stress tolerance of the plants directly. AtCML19, a kind of CML, showed repair function of cell damage caused by UV irradiation (Molinier et al. 2004).

Specifically, CDPKs were found to enhance Cd tolerance in *Arabidopsis thaliana* through intensifying H_2S signal (Qiao et al. 2016). The experimental evidence for Ca-dependent signaling in the regulation of Cd stress in plants is still lacking. But it has been reported that Ca signals could trigger numerous defense reactions in plants which certainly will help plants better cope with Cd stress. For instance, researches have confirmed the function of Ca-dependent signaling in the regulation of plant photosynthesis and respiration (Islam et al. 2010), which might enhance plants Cd-tolerance by the regulation of plant physiological processes. Furthermore, it has been reported that Ca-signaling could mediate cell response to Cd toxicity and it also could participate in the regulation of Cd-induced cytotoxicity and cell death (Jiang et al. 2015; Ruta et al. 2014). Besides, the interaction between Ca signatures and ROS waves has unraveled a new pathway of the oxidative damage alleviation in the organisms (Gilroy et al. 2014; Steinhorst and Kudla 2014), and this may provide another possible mechanism to better illustrated the function of Ca in the alleviation of Cd-induced oxidative stress. Further detailed researches are required to elucidate the precise role of Ca-dependent signaling in the amelioration of Cd-induced toxicity.

Other possible mechanisms

Several studies have provided other possible mechanisms regarding the influence of exogenously applied Ca on Cd toxicity. Choi and Harada (2005) studied the roles of Ca on Cd toxicity to tobacco, and they found that the extra and intracellular sequestration of Cd via Ca crystallization could ameliorate Cd-induced damages in the plants. Moreover, a cross-talk between Cd, Ca and nitric oxide (NO) has been observed in plants. The application of Cd depressed NO production strongly in pea plant cells, and the addition of Ca retarded this effect, thus protecting plant cells against Cd-induced toxicity (Rodriguez-Serrano et al. 2009). Likewise, the application of Ca increased the endogenous NO levels under Cd stress in rice seedlings, and, thereby, influenced Cd transport in plant cells. The results indicated that Ca could protect plants against the deleterious effects of Cd via the generation of NO (Zhang et al. 2012). Additionally, it has been demonstrated that the occurrence of autophagy induced by Cd in plant cells could be prevented by the pre-treatment of Ca (Andosch et al. 2012). Meanwhile, the increased accumulation of the protective substances, such as the total soluble protein, proline and pectin, triggered by Ca could also ameliorate Cd-induced toxicity in plants. For example, Ca application ameliorated the harmful effects of Cd in *B. juncea* by enhancing the contents of proline in plants leaves (Hayat et al. 2015). Furthermore, Ca also plays an important role in the modification of glyoxalase system and it could reduce methylglyoxal toxicity in plants under Cd stress (Rahman et al. 2016).

Conclusions and perspectives

The present review covers the roles of Ca in the plants under heavy metal stress, which emphasizes the effects of Ca on plant growth, metal accumulation and translocation, photosynthesis, oxidative damage and signal transduction under Cd stress. The review also provides new insight that Ca could be used as an exogenous substance to ameliorate the harmful effects of Cd and to improve the phytoremediation efficiency of Cd contaminated soil (Fig. 1). Meanwhile, in this review, we present several mechanisms to certify the protective role of Ca in the alleviation of Cd toxicity, and these mechanisms could be further applied to explore the influences of other exogenous substances to plants under environmental stress, thus finding new approaches to improve plant resistance and enhance phytoremediation efficiency.

Many researchers have made great efforts to clarify the roles of exogenous substances in the alleviation of heavy metal toxicity to plants. However, the impacts of exogenous substances could be affected by many factors, and the related mechanisms were still unclear and debatable. Therefore, further studies are needed to find the most suitable conditions for the application of exogenous substances and to explore the unrevealed mechanisms of the exogenous substances in the mitigation of heavy metal induced toxicity. Besides, novel methods and techniques, such as fluorescent tracer technique, should be developed and utilized to visualize the uptake and distribution of exogenous substances and the target pollutants in the plans quantitatively and qualitatively. Moreover, knowledge of the molecular and genetic mechanisms by which exogenous substances help plants better cope with heavy metal stress is limited. Further in-depth physiological, molecular and genetic studies are needed to provide a more comprehensive explanation of the impacts of exogenous substances on heavy metal induced toxicity in plants.

Author contribution statement DH, XG, YL and GZ conceived the review. XG wrote the manuscript. CL, HB and LZ collected relevant information and data. DW, PX, MC and JW provided grammatical and style corrections. All authors read and approved this manuscript.

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References

Ahmad P, Sarwat M, Bhat NA, Wani MR, Kazi AG, Tran LS (2015) Alleviation of cadmium toxicity in *Brassica juncea* L. (Czern. & Coss.) by calcium application involves various physiological and biochemical strategies. PLoS One 10(1):e0114571

Ajm B, Whiting SN (2002) In search of the Holy Grail—a further step in understanding metal hyperaccumulation? New Phytol 155(1):1–4

Ali H, Khan E, Sajad MA (2013) Phytoremediation of heavy metals—concepts and applications. Chemosphere 91(7):869–881

Andosch A, Affenzeller MJ, Lutz C, Lutz-Meindl U (2012) A freshwater green alga under cadmium stress: ameliorating calcium effects on ultrastructure and photosynthesis in the unicellular model *Micrasterias*. J Plant Physiol 169(15):1489–1500

Ansari MM, Neha, Khan HA (2015) Effect of cadmium chloride exposure during the induction of collagen induced arthritis. Chem Biol Interact 238:55–65

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Baliardini C, Meyer CL, Salis P, Saumitoulaprade P, Verbruggen N (2015) CATION EXCHANGER1 cosegregates with cadmium tolerance in the metal hyperaccumulator *Arabidopsis halleri* and plays a role in limiting oxidative stress in *Arabidopsis* spp. Plant Physiol 169(1):549–559

Bartlett JE, Baranov SV, Ananyev GM, Dismukes GC (2008) Calcium controls the assembly of the photosynthetic water-oxidizing complex: a cadmium(II) inorganic mutant of the Mn4Ca core. Philos Trans R Soc Lond B Biol Sci 363(1494):1253–1261

Bhargava A, Carmona FF, Bhargava M, Srivastava S (2012) Approaches for enhanced phytoextraction of heavy metals. J Environ Manag 105:103–120

Brand JJ, Becker DW (1984) Evidence for direct roles of calcium in photosynthesis. J Bioenerg Biomembr 16(4):239–249

Brodziak-Dopierała B, Kwapuliński J, Sobczyk K, Wiechuła D (2015) Analysis of the content of cadmium and zinc in parts of the human hip joint. Biol Trace Elem Res 163(1–2):73–80

Brunetti P, Zanella L, Proia A, De PA, Falasca G, Altamura MM, Sanità DTL, Costantino P, Cardarelli M (2011) Cadmium tolerance and phytochelatin content of *Arabidopsis* seedlings over-expressing the phytochelatin synthase gene AtPCS1. J Exp Bot 62(15):5509–5519

Buhlungu BP, Ntoni NJ (2002) Phytoremediation of cadmium-contaminated soils using *Leonotis leonurus*. Folia Cardiol 9(6):545–551

Cao D-j, X-d Shi, Li H, P-p Xie, H-m Zhang, J-w Deng, Y-g Liang (2015) Effects of lead on tolerance, bioaccumulation, and antioxidative defense system of green algae, Cladophora. Ecotox Environ Safe 112:231–237

Chang Y-S, Chang Y-J, Lin C-T, Lee M-C, Wu C-W, Lai Y-H (2013) Nitrogen fertilization promotes the phytoremediation of cadmium in *Pentas lanceolata*. Int Biodeter Biodegr 85:709–714

Chao Y-Y, Hong C-Y, Chen C-Y, Kao CH (2011) The importance of glutathione in defence against cadmium-induced toxicity of rice seedlings. Crop Environ Bioinform 8:217–228

Cheng K, Tian HZ, Zhao D, Lu L, Wang Y, Chen J, Liu XG, Jia WX, Huang Z (2014) Atmospheric emission inventory of cadmium from anthropogenic sources. Int J Environ Sci Technol 11(3):605–616

Cho S-C, Chao Y-Y, Kao CH (2012) Calcium deficiency increases Cd toxicity and Ca is required for heat-shock induced Cd tolerance in rice seedlings. J Plant Physiol 169(9):892–898

Choi Y-E, Harada E (2005) Roles of calcium and cadmium on Cd-containing intra-and extracellular formation of Ca crystals in tobacco. J Plant Biol 48(1):113–119

Connolly EL, Fett JP, Guerinot ML (2002) Expression of the IRT1 metal transporter is controlled by metals at the levels of transcript and protein accumulation. Plant Cell 14(6):1347–1357

Dayod M, Tyerman SD, Leigh RA, Gilliham M (2010) Calcium storage in plants and the implications for calcium biofortification. Protoplasma 247(3–4):215–231

Degl'Innocenti E, Castagna A, Ranieri A, Guidi L (2014) Combined effects of cadmium and ozone on photosynthesis of *Lycopersicon esculentum*. Photosynthetica 52(2):179–185

Deng G, Li M, Li H, Yin L, Li W (2014) Exposure to cadmium causes declines in growth and photosynthesis in the endangered aquatic fern (*Ceratopteris pteridoides*). Aquat Bot 112:23–32

Dias MC, Monteiro C, Moutinho-Pereira J, Correia C, Gonçalves B, Santos C (2012) Cadmium toxicity affects photosynthesis and plant growth at different levels. Acta Physiol Plan 35(4):1281–1289

El-Beltagi HS, Mohamed HI (2013) Alleviation of cadmium toxicity in *Pisum sativum* L. seedlings by calcium chloride. Not Bot Hortic Agrobot 41(1):157–168

El-Enany AE (1995) Alleviation of cadmium toxicity on maize seedlings by calcium. Biol Plant 37(1):93–99

Eller F, Brix H (2016) Influence of low calcium availability on cadmium uptake and translocation in a fast-growing shrub and a metal-accumulating herb. Aob Plants 8. doi:10.1093/aobpla/plv143

Fagerberg B, Barregard L, Sallsten G, Forsgard N, Östling G, Persson M, Borné Y, Engström G, Hedblad B (2015) Cadmium exposure and atherosclerotic carotid plaques—results from the Malmö diet and Cancer study. Environ Res 136:67–74

Faller P, Kienzler K, Krieger-Liszkay A (2005) Mechanism of Cd^{2+} toxicity: Cd^{2+} inhibits photoactivation of photosystem II by competitive binding to the essential Ca^{2+} site. Biochim Biophys Acta 1706(1–2):158–164

Farzadfar S, Zarinkamar F, Modarres-Sanavy S, Hojati M (2013) Exogenously applied calcium alleviates cadmium toxicity in *Matricaria chamomilla* L. plants. Environ Sci Pollut Res 20(3):1413–1422

Gallego SM, Benavídes MP, Tomaro ML (1996) Effect of heavy metal ion excess on sunflower leaves: evidence for involvement of oxidative stress. Plant Sci 121(2):151–159

Gilroy S, Suzuki N, Miller G, Choi WG, Toyota M, Devireddy AR, Mittler R (2014) A tidal wave of signals: calcium and ROS at the forefront of rapid systemic signaling. Trends Plant Sci 19(10):623–630

Gong X, Liu Y, Huang D, Zeng G, Liu S, Tang H, Zhou L, Hu X, Zhou Y, Tan X (2016) Effects of exogenous calcium and spermidine on cadmium stress moderation and metal accumulation in *Boehmeria nivea* (L.) Gaudich. Environ Sci Pollut Res 23:8699–8708

Hashimoto K, Kudla J (2011) Calcium decoding mechanisms in plants. Biochimie 93(12):2054–2059

Hayakawa N, Tomioka R, Takenaka C (2011) Effects of calcium on cadmium uptake and transport in the tree species *Gamblea innovans*. Soil Sci Plant Nutr 57(5):691–695

Hayat S, Ahmad A, Wani AS, Alyemeni MN, Ahmad A (2015) Regulation of growth and photosynthetic parameters by salicylic acid and calcium in *Brassica juncea* under cadmium stress. Z Naturforsch 69:452–458

Heyno E, Klose C, Krieger-Liszkay A (2008) Origin of cadmium-induced reactive oxygen species production: mitochondrial electron transfer versus plasma membrane NADPH oxidase. New Phytol 179(3):687–699

Hirschi KD (2004) The calcium conundrum. Both versatile nutrient and specific signal. Plant Physiol 136(1):2438–2442

Hochmal AK, Schulze S, Trompelt K, Hippler M (2015) Calcium-dependent regulation of photosynthesis. Biochim Biophys Acta 1847(9):993–1003

Hong Y, Yan S (2015) Cadmium transporters in the kidney and cadmium-induced nephrotoxicity. Int J Mol Sci 16(1):1484–1494

Huang DL, Zeng GM, Feng CL, Hu S, Jiang XF, Tang L, Su FF, Zhang Y, Zeng W, Liu HL (2008) Degradation of lead-contaminated lignocellulosic waste by *Phanerochaete chrysosporium* and the reduction of lead toxicity. Environ Sci Technol 42:4946–4951

Huang DL, Wang RZ, Liu YG, Zeng GM, Lai C, XuP LuBA, Xu JJ, Wang C, Huang C (2015) Application of molecularly imprinted polymers in wastewater treatment: a review. Environ Sci Pollut Res 22(2):963–977

Huang DL, Xue WJ, Zeng GM, Wan J, Chen GM, Huang C, Zhang C, Cheng M, Xu P (2016) Immobilization of Cd in river sediments by sodium alginate modified nanoscale zero-valent iron: impact on enzyme activities and microbial community diversity. Water Res 106:15–25

Huda KM, Banu MS, Tuteja R, Tuteja N (2013) Global calcium transducer P-type Ca^{2+}-ATPases open new avenues for agriculture by regulating stress signalling. J Exp Bot 64(11):3099–3109

Iannelli MA, Pietrini F, Fiore L, Petrilli L, Massacci A (2002) Antioxidant response to cadmium in Phragmites australis plants. Plant Physiol Biochem 40(11):977–982

Islam MM, Munemasa S, Hossain MA, Nakamura Y, Mori IC, Murata Y (2010) Roles of AtTPC1, vacuolar two pore channel 1. Arabidopsis stomatal closure. Plant Cell Physiol 51(2):302–311

Islam MS, Ahmed MK, Raknuzzaman M, Habibullah-Al-Mamun M, Islam MK (2015) Heavy metal pollution in surface water and sediment: a preliminary assessment of an urban river in a developing country. Ecol Indic 48:282–291

Jarup L (2003) Hazards of heavy metal contamination. Brit Med Bull 68(1):167–182

Jiali H, Hong L, Jie L, Chaofeng M, Shaojun L, Long Q, Ying G, Xiangning J, Janz D, Polle A, Tyree M, Zhi-Bin L (2013) A transcriptomic network underlies microstructural and physiological responses to cadmium in *Populus* × *canescens*. Plant Physiol 162(1):424–439

Jiang JH, Ge G, Gao K, Pang Y, Chai RC, Jia XH, Kong JG, Yu AC-H (2015) Calcium signaling involvement in cadmium-induced astrocyte cytotoxicity and cell death through activation of MAPK and PI3K/Akt signaling pathways. Neurochem Res 40(9):1929–1944

Jones RGW, Lunt OR (1967) The function of calcium in plants. Bot Rev 33(4):407–426

Kärkönen A, Kuchitsu K (2015) Reactive oxygen species in cell wall metabolism and development in plants. Phytochemistry 112:22–32

Kastori R, Petrović M, Petrović N (1992) Effect of excess lead, cadmium, copper, and zinc on water relations in sunflower. J Plant Nutr 15(11):2427–2439

Kesseler A, Brand M (1995) The mechanism of the stimulation of state 4 respiration by cadmium in potato tuber (*Solanum tuberosum*) mitochondria. Plant Physiol Biochem 33(4):519–528

Kim YY, Yang YY, Lee Y (2002) Pb and Cd uptake in rice roots. Physiol Plant 116(3):368–372

Kinraid TB (1998) Three mechanisms for the calcium alleviation of mineral toxicities. Plant Physiol 118(2):513–520

Koptsik GN (2014) Problems and prospects concerning the phytoremediation of heavy metal polluted soils: a review. Eurasian Soil Sci 47(9):923–939

Kováčik J (2013) Hyperaccumulation of cadmium in *Matricaria chamomilla*: a never-ending story? Acta Physiol Plant 35(5):1721–1725

Kumar M, Kumari P, Gupta V, Anisha PA, Reddy CRK, Jha B (2010) Differential responses to cadmium induced oxidative stress in marine macroalga *Ulva lactuca* (Ulvales, Chlorophyta). Biometals 23(2):315–325

Kurtyka R, Małkowski E, Kita A, Karcz W (2008) Effect of Calcium and Cadmium onGrowth and Accumulation of Cadmium, Calcium, Potassium and Sodium in Maize Seedlings. Polish J Environ Stud 17:51–56

Lecourieux D, Ranjeva R, Pugin A (2006) Calcium in plant defence-signalling pathways. New Phytol 171(2):249–269

Lehmann S, Serrano M, L'Haridon F, Tjamos SE, Metraux J-P (2015) Reactive oxygen species and plant resistance to fungal pathogens. Phytochemistry 112:54–62

Li H, Liu Y, Zeng G, Zhou L, Wang X, Wang Y, Wang C, Hu X, Xu W (2014) Enhanced efficiency of cadmium removal by *Boehmeria nivea* (L.) Gaud. in the presence of exogenous citric and oxalic acids. J Environ Sci 26(12):2508–2516

Li P, Zhao C, Zhang Y, Wang X, Wang X, Wang J, Wang F, Bi Y (2015a) Calcium alleviates cadmium-induced inhibition on root growth by maintaining auxin homeostasis in Arabidopsis seedlings. Protoplasma 253:185–200

Li S, Yang W, Yang T, Chen Y, Ni W (2015b) Effects of cadmium stress on leaf chlorophyll fluorescence and photosynthesis of *Elsholtzia argyi*—a cadmium accumulating plant. Int J Phytoremed 17(1):85–92

Li X, Zhou Q, Sun X, Ren W (2016) Effects of cadmium on uptake and translocation of nutrient elements in different welsh onion (*Allium fistulosum* L.) cultivars. Food Chem 194:101–110

Liu Y, Xin W, Zeng G, Dan Q, Gu J, Ming Z, Chai L (2007) Cadmium-induced oxidative stress and response of the ascorbate–glutathione cycle in *Bechmeria nivea* (L.) Gaud. Chemosphere 69(1):99–107

Liu W, Shang S, Feng X, Zhang G, Wu F (2015) Modulation of exogenous selenium in cadmium-induced changes in antioxidative metabolism, cadmium uptake, and photosynthetic performance in the 2 tobacco genotypes differing in cadmium tolerance. Environ Toxicol Chem 34(1):92–99

López ML, Peralta-Videa JR, Benitez T, Gardea-Torresdey JL (2005) Enhancement of lead uptake by alfalfa (*Medicago sativa*) using EDTA and a plant growth promoter. Chemosphere 61(4):595–598

López ML, Peralta-videa JR, Parsons JG, Benitez T, Gardea-Torresdey JL (2007) Gibberellic acid, kinetin, and the mixture indole—3-acetic acid—kinetin assisted with EDTA-induced lead hyperaccumulation in alfalfa plants. Environ Sci Technol 41(23):8165–8170

Lopez-Climent MF, Arbona V, Perez-Clemente RM, Zandalinas SI, Gomez-Cadenas A (2013) Effect of cadmium and calcium treatments on phytochelatin and glutathione levels in citrus plants. Plant Biol 16(1):79–87

Luo J, Qi S, Peng L, Xie X (2015) Phytoremediation potential of cadmium-contaminated soil by *Eucalyptus globulus* under different coppice systems. Bull Environ Contam Toxicol 94(3):321–325

Marchetti C (2013) Role of calcium channels in heavy metal toxicity. ISRN Toxicol 2013:184360

Miqyass M, van Gorkom HJ, Yocum CF (2007) The PSII calcium site revisited. Photosynth Res 92(3):275–287

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7(9):405–410

Mleczek M, Kozlowska M, Kaczmarek Z, Chadzinikolau T, Golinski P (2012) Influence of Ca/Mg ratio on phytoextraction properties of *Salix viminalis* I. The effectiveness of Cd, Cu, Pb, and Zn bioaccumulation and plant growth. Int J Phytoremed 14(1):75–88

Mohamed FI (2012) Protective effects of some antioxidant metals against chromosomal damage induced by cadmium in *Vicia faba* plants. Int J Agric Res 7:376–387

Molinier J, Ramos C, Fritsch O, Hohn B (2004) CENTRIN2 modulates homologous recombination and nucleotide excision repair in arabidopsis. Plant Cell 16(6):1633–1643

Nedjimi B, Daoud Y (2009) Cadmium accumulation in *Atriplex halimus* subsp. *schweinfurthii* and its influence on growth, proline, root hydraulic conductivity and nutrient uptake. Flora Morphol Distrib Funct Ecol Plants 204(4):316–324

Obata H, Umebayashi M (1997) Effects of cadmium on mineral nutrient concentrations in plants differing in tolerance for cadmium. J Plant Nutr 20(1):97–105

Parvaiz A, Abdel LAA, Abd Allah EF, Abeer H, Maryam S, Anjum NA, Salih G (2016) Calcium and potassium supplementation enhanced growth, osmolyte secondary metabolite production, and enzymatic antioxidant machinery in cadmium-exposed chickpea (*Cicer arietinum* L.). Front Plant Sci 7:347

Perez-Chaca MV, RodrÍGuez-Serrano M, Molina AS, Pedranzani HE, Zirulnik F, Sandalio LM, Romero-Puertas MC (2014) Cadmium induces two waves of reactive oxygen species in *Glycine max* (L.) roots. Plant Cell Environ 37(7):1672–1687

Perfus-Barbeoch L, Leonhardt N, Vavasseur A, Forestier C (2002) Heavy metal toxicity: cadmium permeates through calcium channels and disturbs the plant water status. Plant J 32(32):539–548

Piterková J, Luhová L, Navrátilová B, Sedlářová M, Petřivalský M (2015) Early and long-term responses of cucumber cells to high cadmium concentration are modulated by nitric oxide and reactive oxygen species. Acta Physiol Plant 37(2):1–12

Qiao Z, Jing T, Jin Z, Liang Y, Zhang L, Liu Z, Liu D, Pei Y (2016) CDPKs enhance Cd tolerance through intensifying H2S signal in *Arabidopsis thaliana*. Plant Soil 398(1–2):99–110

Rahman A, Mostofa MG, Nahar K, Hasanuzzaman M, Fujita M (2016) Exogenous calcium alleviates cadmium-induced oxidative stress in rice (*Oryza sativa* L.) seedlings by regulating the antioxidant defense and glyoxalase systems. Braz J Bot 39(2):393–407

Ramalho JC, Rebelo MC, Santos ME, Antunes ML, Nunes M (1994) Effects of calcium deficiency on *Coffea arabica*. Nutrient changes and correlation of calcium levels with some photosynthetic parameters. Plant Soil 172(1):87–96

Rodriguez-Hernandez MC, Bonifas I, Alfaro-De la Torre MC, Flores-Flores JL, Bañuelos-Hernández B, Patiño-Rodríguez O (2015) Increased accumulation of cadmium and lead under Ca and Fe deficiency in *Typha latifolia*: a study of two pore channel (TPC1) gene responses. Environ Exp Bot 115:38–48

Rodriguez-Serrano M, Romero-Puertas MC, Pazmino DM, Testillano PS, Risueno MC, Del Rio LA, Sandalio LM (2009) Cellular response of pea plants to cadmium toxicity: cross talk between reactive oxygen species, nitric oxide, and calcium. Plant Physiol 150(1):229–243

Ruta LL, Popa VC, Nicolau I, Danet AF, Iordache V, Neagoe AD, Farcasanu IC (2014) Calcium signaling mediates the response to cadmium toxicity in *Saccharomyces cerevisiae* cells. FEBS Lett 588(17):3202–3212

Saed-Moucheshi A, Shekoofa A, Pessarakli M (2014) Reactive oxygen species (ROS) generation and detoxifying in plants. J Plant Nutr 37(10):1573–1585

Sakan SM, Dević GJ, Relić DJ, Anđelković IB, Sakan NM, Đorđević DS (2015) Environmental assessment of heavy metal pollution in freshwater sediment, Serbia. Clean Soil Air Water 43(6):838–845

Salt DE, Prince RC, Pickering IJ, Raskin I (1995) Mechanisms of cadmium mobility and accumulation in Indian mustard. Plant Physiol 109(4):1427–1433

Sasaki A, Ma JF (2012) Nramp5 is a major transporter responsible for manganese and cadmium uptake in rice. Plant Cell 24(5):2155–2167

Shahid M, Austruy A, Echevarria G, Arshad M, Sanaullah M, Aslam M, Nadeem M, Nasim W, Dumat C (2014) EDTA-enhanced phytoremediation of heavy metals: a review. Soil Sediment Contam 23(4):389–416

Shi HP, Zhu YF, Wang YL, Tsang PK (2014) Effect of cadmium on cytogenetic toxicity in hairy roots of *Wedelia trilobata* L. and their alleviation by exogenous $CaCl_2$. Environ Sci Pollut Res Int 21(2):1436–1443

Siddiqui MH, Al-Whaibi MH, Sakran AM, Basalah MO, Ali HM (2012) Effect of calcium and potassium on antioxidant system of *Vicia faba* L. under cadmium stress. Int J Mol Sci 13(6):6604–6619

Singh A, Prasad SM (2014) Remediation of heavy metal contaminated ecosystem: an overview on technology advancement. Int J Environ Sci Technol 12(1):353–366. doi:10.1007/s13762-014-0542-y

Skórzyńska-Polit E, Tukendorf A, Selstam E, Baszyński T (1998) Calcium modifies Cd effect on runner bean plants. Environ Exp Bot 40(3):275–286

Spirlandeli AL, Deminice R, Jordao AA (2014) Plasma malondialdehyde as biomarker of lipid peroxidation: effects of acute exercise. Int J Sports Med 35(1):14–18

Srivastava RK, Pandey P, Rajpoot R, Rani A, Gautam A, Dubey RS (2015) Exogenous application of calcium and silica alleviates cadmium toxicity by suppressing oxidative damage in rice seedlings. Protoplasma 252(4):959–975

Steinhorst L, Kudla J (2014) Signaling in cells and organisms—calcium holds the line. Curr Opin Plant Biol 22:14–21

Stockinger EJ, Skinner JS, Gardner KG, Francia E, Pecchioni N (2007) Expression levels of barley Cbf genes at the Frost resistance-H2 locus are dependent upon alleles at Fr-H1 and Fr-H2. Plant J 51(2):308–321

Stravinskienė V, Račaitė M (2014) Impact of cadmium and zinc on the growth of white clover (*Trifolium repens* L.) shoots and roots. Pol J Environ Stud 23(4):1355–1359

Suzuki N (2005) Alleviation by calcium of cadmium-induced root growth inhibition in Arabidopsis seedlings. Plant Biotechnol 22(1):19–25

Talukdar D (2012) Exogenous calcium alleviates the impact of cadmium-induced oxidative stress in *Lens culinaris* Medic. seedlings through modulation of antioxidant enzyme activities. J Crop Sci Biotechnol 15(4):325–334

Tang H, Liu Y, Gong X, Zeng G, Zheng B, Wang D, Sun Z, Zhou L, Zeng X (2015) Effects of selenium and silicon on enhancing antioxidative capacity in ramie (*Boehmeria nivea* (L.) Gaud.) under cadmium stress. Environ Sci Pollut Res 22(13):9999–10008

Tian S, Lu L, Zhang J, Wang K, Brown P, He Z, Liang J, Yang X (2011) Calcium protects roots of *Sedum alfredii* H. against cadmium-induced oxidative stress. Chemosphere 84(1):63–69

Tran TA, Popova LP (2013) Functions and toxicity of cadmium in plants: recent advances and future prospects. Turk J Bot 37(1):1–13

Wan G, Najeeb U, Jilani G, Naeem MS, Zhou W (2011) Calcium invigorates the cadmium-stressed *Brassica napus* L. plants by strengthening their photosynthetic system. Environ Sci Pollut Res 18(9):1478–1486

Wang CL, Liu YG, Zeng GM, Xin-Jiang HU, Ying YC, Xi HU, Zhou L, Wang YQ, Hua-Ying LI (2014) Mechanism of exogenous selenium alleviates cadmium induced toxicity in *Bechmeria nivea* (L.) Gaud (Ramie). Trans Nonferr Metal Soc 24(12):3964–3970

Wang D, Liu Y, Tan X, Liu H, Zeng G, Hu X, Jian H, Gu Y (2015) Effect of exogenous nitric oxide on antioxidative system and S-nitrosylation in leaves of *Boehmeria nivea* (L.) Gaud under cadmium stress. Environ Sci Pollut Res 22(5):3489–3497

Xu P, Liu L, Zeng G, Huang D, Lai C, Zhao M, Huang C, Li N, Wei Z, Wu H, Zhang C, Lai M, He Y (2014) Heavy metal-induced glutathione accumulation and its role in heavy metal detoxification in *Phanerochaete chrysosporium*. Appl Microbiol Biotechnol 98(14):6409–6418

Xu P, Zeng G, Huang D, Dong H, Lai C, Chen M, Tang W, Li F, Leng Y, Cheng M, He X, He Y (2015) Cadmium induced hydrogen peroxide accumulation and responses of enzymatic antioxidants in *Phanerochaete chrysosporium*. Ecol Eng 75:110–115

Yang CM, Juang KW (2015) Alleviation effects of calcium and potassium on cadmium rhizotoxicity and absorption by soybean and wheat roots. J Plant Nutr Soil Sci 178(5):748–754

Yang J, Kim E-C, Shin D-C, Jo S-J, Lim Y-W (2015a) Human exposure and risk assessment of cadmium for residents of abandoned metal mine areas in Korea. Environ Geochem Health 37(2):321–332

Yang X, Duan J, Wang L, Li W, Guan J, Beecham S, Mulcahy D (2015b) Heavy metal pollution and health risk assessment in the Wei River in China. Environ Monit Assess 187(3):1–11

Zhang W, Zhou R-G, Gao Y-J, Zheng S-Z, Xu P, Zhang S-Q, Sun D-Y (2009) Molecular and genetic evidence for the key role of AtCaM3 in heat-shock signal transduction in arabidopsis. Plant Physiol 149(4):1773–1784

Zhang L, Chen Z, Zhu C (2012) Endogenous nitric oxide mediates alleviation of cadmium toxicity induced by calcium in rice seedlings. J Environ Sci 24(5):940–948

Zhang SJ, Li TX, Huang HG, Zhang XZ, Yu HY, Zheng ZC, Wang YD, Zou TJ, Hao XQ, Pu Y (2014a) Phytoremediation of cadmium using plant species of *Athyrium wardii* (Hook.). Int J Environ Sci Technol 11(3):757–764

Zhang X, Gao B, Xia H (2014b) Effect of cadmium on growth, photosynthesis, mineral nutrition and metal accumulation of bana grass and vetiver grass. Ecotox Environ Safe 106:102–108

Zhang M, Zhang J, Lu LL, Zhu ZQ, Yang XE (2015) Functional analysis of CAX2-like transporters isolated from two ecotypes of *Sedum alfredii*. Biol Plant 60(1):37–47