Lead (Pb) is one of the most widespread heavy metal contaminant in soils. It is highly toxic to living organisms. Pb has no biological function but can cause morphological, physiological, and biochemical dysfunctions in plants. Plants have developed a wide range of tolerance mechanisms that are activated in response to Pb exposure. Pb affects plants primarily through their root systems. Plant roots rapidly respond either (i) by the synthesis and deposition of callose, creating a barrier that stops Pb entering (ii) through the uptake of large amounts of Pb and its sequestration in the vacuole accompanied by changes in root growth and branching pattern or (iii) by its translocation to the aboveground parts of plant in the case of hyperaccumulators plants. Here we review the interactions of roots with the presence of Pb in the rhizosphere and the effect of Pb on the physiological and biochemical mechanisms of root development.

**Keywords:** root, lead, tolerance, uptake, root development
AVAILABLE UPTAKE OF LEAD BY ROOTS
The rhizosphere is where interactions take place between roots and soil constituents (Lynch and Withers, 1990). When a root absorbs water or nutrients from soil, ions and molecules move toward this organ both by mass flow with soil water and by diffusion (Robinson, 1991). Pb may be present in different fractions in the soils. It was previously thought that Pb had low solubility and availability for plant uptake because it forms precipitates with phosphates, sulfates, and chemicals in the rhizosphere (Blaylock and Huang, 2000). These geo-chemical forms of Pb in soils affect its solubility, which directly influences its mobility. However, roots produce and excrete protons, exuates and several metabolites, which can modify the soil pH and thus interfere with the dissolution processes and formation of soluble metal-organic complexes (Leyval and Berthelin, 1991). Citric, fumaric, and uronic acids as well as many polysaccharides are able to form complexes and to chelate metal ions including Pb (Mench et al., 1987). Indeed, in Vicia faba and Typha angustifolia, Pb uptake by roots was shown to increase significantly in the first hour after adding organic ligands (ethylene diaminetetraacetic acid (EDTA), citric acid; Muhammad et al., 2009; Shahid et al., 2012). However, Quartacci et al. (2006) reported that citric acid supplied to a metal contaminated soil did not cause any change in metal uptake in Brassica juncea.

Lead uptake is greatly affected by rhizospheric processes. Lin et al. (2004) explained the ability of Oryza sativa L. to absorb high levels of Pb from soil by a decrease in soil pH due to root exudates, solubilization of Pb by rhizosphere microorganisms and complexation of Pb with organic matter at the soil-root interface. These authors also found larger amounts of NH4OAc extractable Pb in the rhizosphere than in bulk soil, pointing to the involvement of solubilization of Pb by rhizosphere microorganisms and complexation. In response to Pb exposure, plants have developed a variety of tolerance mechanisms (Figure 1). Roots are the first organs, exposed to Pb ions (Piocholak et al., 2002). The first defense strategy is to stop the metal entering the root tissues by excluding it (Mishra et al., 2011). Samardakiewicz et al. (2012) examined whether callose forms an efficient barrier against Pb penetration in the roots of Lemma minor L. exposed to 15 μM of Pb for 6 h. This treatment resulted in the synthesis and deposition of callose in the newly formed cell wall in the protoderm in the center of the root tip. After callose deposition the Pb concentration was restricted in these superficial cells. Similar observations have been made in other species exposed to Pb including Arabidopsis thaliana (Limmerchheim et al., 1995) and Funaria hygrometrica (Krzesłowska et al., 2009). Pb-induced callose deposition has been detected in the rhizodermis and in the center of the stele of Pb-treated soybean Glycine max roots tips (Samardakiewicz et al., 1996). Under metal stress, the synthesized callose inhibits cell-to-cell transport.

**ROOT DEFENSE AGAINST LEAD STRESS**
In response to Pb exposure, plants have developed a variety of tolerance mechanisms (Figure 1). Roots are the first organs, exposed to Pb ions (Piocholak et al., 2002). The first defense strategy is to stop the metal entering the root tissues by excluding it (Mishra et al., 2011). Samardakiewicz et al. (2012) examined whether callose forms an efficient barrier against Pb penetration in the roots of Lemma minor L. exposed to 15 μM of Pb for 6 h. This treatment resulted in the synthesis and deposition of callose in the newly formed cell wall in the protoderm in the center of the root tip. After callose deposition the Pb concentration was restricted in these superficial cells. Similar observations have been made in other species exposed to Pb including Arabidopsis thaliana (Limmerchheim et al., 1995) and Funaria hygrometrica (Krzesłowska et al., 2009). Pb-induced callose deposition has been detected in the rhizodermis and in the center of the stele of Pb-treated soybean Glycine max roots tips (Samardakiewicz et al., 1996). Under metal stress, the synthesized callose inhibits cell-to-cell transport.

**Figure 1** | Schematic representation of the types of root responses to lead toxicity in higher plants. (a) Pb sequestration in the Fe/Mn plaques; (b) Pb binding in callose formed in the new cell wall; (c) Pb fluxes across the plasma membrane; (d) Chelation of Pb in the cytosol by phytochelatins; (e) Transport of PC-Pb complex and sequestration in the vacuole.
This may result in the prevention of a wide incursion of Pb ions, but it can simultaneously inhibit the transport of other molecules. However, the synthesis of callose is not a general pattern in plants in response to Pb, in Zea mays and G. muc, low level Pb treatment did not result in any callose deposition in root tissue. Although, these species synthesized callose in response to cadmium or arsenic (Posoletova et al., 2012). It seems that the formation of callose was closely related to the amount of Pb entering the cell, and subsequently the level of stress.

In some plants, the formation of Fe and Mn plaques on root surface may provide a means of attenuation and external exclusion of metals. These plaques increase the sequestration of Pb on the root surface and in the rhizosphere, providing a means of external exclusion of soil Pb (Hamet et al., 2002). In some rice cultivars, Fe plaques were shown to affect patterns of Pb uptake and accumulation. Lower concentrations of Pb were found in the root tissues of rice plants with plaque compared to concentrations found in the plants without plaque. But the functions of plaque are limited as they are only efficient in relatively low or moderately Pb-contaminated soil (Liu et al., 2011). Fe plaque and plaque are limited as they are only efficient in relatively low or moderately Pb-contaminated soil (Liu et al., 2011). Fe plaque and organic matrix with high Pb affinity were found in root epidermis of Typha latifolia, and were shown to prevent the accumulation and the translocation of Pb within the root (Qian et al., 2012; Feng et al., 2013).

In most plants, 90% of the total Pb is accumulated in roots (Kumar et al., 1995). Most Pb in roots is localized in the insoluble fraction of cell walls and nuclei, which is linked with the detoxification mechanism (Pichalak et al., 2002). After exposure to Pb, cell mechanisms that minimize the potential for toxicity are rapidly activated. In the roots of several species including Pisum sativum (Malecka et al., 2009), Allium sativum (Jiang and Liu, 2010), and Arabidopsis yokescens (Nishizono et al., 1987), the cell walls, the first barrier against Pb stress, can immobilize and accumulate some or even most Pb ions. The important role of the cell wall in the defense response of plants to trace metals was recently reviewed by Krzeslowska (2011). The capacity of cell walls to bind divalent metal cations mainly depends on the amount of polysaccharides with many carboxyl groups (Inoue et al., 2013). In Arabidopsis thaliana, Pb-galacturonic acid fragments were detected in root treated with Pb (Polec-Pawlak et al., 2007). Brunet et al. (2008) showed that root of Lathyrus sativus L. exposed to Pb contained much less calcium than control plants, and explained the reduction in Ca content by the replacement of Ca ions by Pb ions, which have a high affinity for pectin in cell walls. In Raphanus sativus, Pb2+ was also shown to bind to carboxyl groups of pectin in cell walls (Inoue et al., 2013). All the examples described above clearly show that the cell wall is one of the preferred and essential compartments for Pb accumulation, deposition, and sequestration. Therefore, these results shed a new light on the functioning of the cell walls in plant cell defense strategy against Pb. Heavy metals including Pb are likely to enter plant cells via essentials cations transporters. AtHMA3, homologous to a non-selective cation channel, was suggested to enable Pb2+ entry since over-expression of the truncated gene resulted in tolerance to Pb2+ (Guo et al., 2008). Ca2+ was also reported to compete with Pb2+ for entry into rice root cells. When Ca2+ was supplied in the medium, it reduced Pb uptake and toxicity (Kim et al., 2002).

This suggests that Pb enters the root cells via Ca2+/Mg2+ gated channel (Kim et al., 2002). In Allium sativum, as soon as excessive Pb ions enter the cytoplasm, a defense mechanism is activated, protecting the cells against Pb toxicity. Endocytotic and exocytotic processes are involved in these phenomena. The plasma membrane represents a “living” barrier of the cell to free inward diffusion of Pb ions. Imagination of plasmolamella and some vesicles from dicotyledons and endoplasmic reticulum (ER) could prevent the free circulation of Pb ions in the cytoplasm. The vacuole is ultimately one of the main storage sites for metal sequestration (reviewed by Sharma and Dubey, 2005; Clemens, 2006). In Allium sativum roots, cysteine-rich peptides commonly referred as phytochelatins (PCs) were detected only after 2 h of Pb exposure (Jiang and Liu, 2010). This indicates that Pb ions can induce synthesis of PCs. Pichalak et al. (2002) demonstrated that the synthesis of PCs takes place under the influence of Pb ions in root cells of three tested plant species of the Fabaceae family: Pisum sativum, V. faba, and Phaseolus vulgaris. The complex Pc-Pb formed is then transported through the cytosol into the vacuoles (Pichalak et al., 2002). AtHMA3, encoding a Pgp-like-ATPase, a heavy metal transporter, is localized in the vacuolar membrane of root cells in Arabidopsis thaliana (Talke et al., 2006; Morel et al., 2009). This transporter is involved in the transfer of complexed heavy metals, including Pb, from the cytoplasm to the vacuole (Morel et al., 2009). Root length was less affected by Pb in Arabidopsis thaliana plants overexpressing AtHMA3 than in wild-type plants (Morel et al., 2009). B. juncea appears to tolerate high concentrations of Pb thanks to its efficient cell roots vacuolar storage mechanisms. In this species, Pb sequestration was restricted to vacuoles (Meyers et al., 2008). In addition, it was suggested that exposure to Pb causes the production of additional vacuole specifically for Pb storage in the root tips of B. juncea (Meyers et al., 2008). The increase in the production of vacuoles could be regarded as a defense and adaptation strategy to elevated levels of Pb in the root cells. This roots potential storage can be used in phytoremediation processes.

Table 1 shows a list of plant species effective in the accumulation of Pb in roots that could be used in rhizoremediation.
In a metallicolous ecotype of *Elsholtzia argyi*, Pb is found in fine particles dispersed through root cell membranes and cell wall fractions whereas in non-metallicolous roots, most Pb was found as large aggregates deposited in the cell wall fractions. These differences in localization explained why non-metallicolous roots were not able to transfer Pb to above ground parts via the apoplasm (Islam et al., 2007). In some plants, Pb can be transported via vascular tissues to aerial parts (Hanc et al., 2009). In *Seabania drummondii*, Pb is transported to leaves after complexation with acetate, nitrate, and sulfide (Sharma et al., 2004). In tobacco, a cyclic nucleotide gated channel (NCaPAs) was suggested to be involved in Pb transport (Sunkar et al., 2000).

To sum up, Pb pathway may include the following stages in roots: Pb can bound with physical barrier (callose, Fe/Mn plaques, cell wall…). At high concentration, this barrier is broken and the flux of Pb enters the cell through the plasma membrane using the ions transporters. In cytoplasm, Pb is chelated with PCs. The complex formed is then sequestered in the vacuoles. In accumulator plants, Pb can be transported via plleom to aerial parts (Figure 1). Compared to Zn and Cd, very little is known about the molecular mechanisms of acquisition, transport, and accumulation of Pb. This is due first to the characteristics of Pb which precipitates with some components of the culture media making difficult to study its bioavailability to the roots. On the other hand, the lack of model plant for studying the mechanisms of tolerance to this metal. Among the 450 species known as metal hyperaccumulator and tolerant plants, Pb accumulating species are rather exceptional. Recently, Auguy et al. (2013) identified *Hirschfeldia incana*, a member of the Brassicaceae family, as a Pb accumulator plant. They demonstrated that this species, owing to its close genetic proximity to *Arabidopsis*, is a good model to identify genes involved in Pb tolerance and accumulation. This can open up new possibilities for understanding the molecular mechanisms of Pb tolerance in plants.

**EFFECT OF LEAD ON ROOT DEVELOPMENT AND PHYSIOLOGY**

Physiological and ultrastructural effects of Pb

The primary effect of Pb toxicity in plants is a rapid inhibition of root growth, probably due to the inhibition of cell division in the root tip (Eun et al., 2000). It was demonstrated that Pb caused inhibition of cell division in *Lemna minor* roots (Samaradevi and Wosny, 2005). In several plant species, including *Triticum aestivum* (Dey et al., 2007; Kaur et al., 2013), *Z. mays* L. (Kozhevnikova et al., 2009), *Pisum sativum* (Malecka et al., 2009), and *Sodium olfradrii* (Gupta et al., 2010), a decrease in the length and in root dry mass under Pb toxicity have been reported (Munzuroglu and Geckil, 2002). Verma and Dubey (2003) showed that growth of rice roots was significantly inhibited at 0.5–1 mM Pb2⁺; up to 40% reduction in root length was observed in 28-day-old rice seedlings. In Pb-treated *Elsholtzia argyi* and *Elsholtzia splendens*, the length and surface area of roots were strongly affected (Peng et al., 2003).

In response to Pb exposure, roots can also respond via changes in volume and diameter, with the production or inhibition of lateral roots. Root cells viability in rice is affected by Pb2⁺ ions and cell death increased at different Pb concentrations (Huang and Huang, 2008). Furthermore, cell wall distention, formation of folds, protuberances, and nicks were observed in response to different Pb concentrations in *Triticum aestivum* (Kaur et al., 2013), *Elsholtzia argyi* (Islam et al., 2007), and *Allium cepa* (Wierzbicka, 1998). Pb has been reported to disrupt microtubulae and microtubules, resulting in the formation of folds (Liu et al., 2009). In addition, Kaur et al. (2013) observed distortions and lesions in cell wall of *Triticum aestivum* roots as a result of activation of certain wall-degrading enzymes in response to Pb exposure. In *Z. mays* roots, Pb treatment resulted in Pb accumulation in the meristem in both apoplastic and symplastic pathways, associated with changes in microtubule organization (Eun et al., 2000).

Lead also has an impact on mineral homeostasis. Brunet et al. (2008) found that roots of *Lathyrus sativus* exposed to Pb showed an increase in Pb content along with an increase in Na levels, which is absorbed to compensate the loss in K. A reduction in Ca contents in Pb-exposed plants has also been observed in other species, such as main, tomato, and mustard varieties (White and Broadley, 2003; Sharma and Dubey, 2005) and could result from the inhibition of Ca transporters by Pb ions (Wojas et al., 2007) and/or replacement of Ca ions with Pb ions due to its high affinity for Ca binding sites on biological structures (Habermann et al., 1983). A reduction in Zn, Cu, and K contents in response to Pb exposure was observed in *Cucumis sativus* and *Z. mays* plants, as a result of a possible blockage of the transporter proteins by Pb (Sharma and Dubey, 2005).

Finally, Pb induces genotoxicity in plants (Rucitska et al., 2004). The comet assay evaluating the DNA-damaging effect of Pb showed an increase in DNA damage in root nuclei of tobacco and lupin (Rucitska et al, 2004; Gichier, 2008).

**BIOCHEMICAL EFFECTS OF LEAD**

The cytotoxic mechanisms of Pb in plants are not entirely understood. It has been reported that Pb leads to the overproduction of reactive oxygen species (ROS) such as superoxide radicals (radical O₂⁻) and hydrogen peroxide (H₂O₂) in plant cells (Reddy et al., 2005; Liu et al., 2010). These can cause lipid peroxidation, membrane damages, and oxidative stress (Sharma and Dietz, 2009). When pro (Pisum sativum) roots were exposed to 0.1 and 0.5 mM of Pb(NO₃)₂, a rapid increase in superoxide anion (O₂⁻) and H₂O₂ levels occurs after 2 and 8 h of Pb treatment, respectively (Malecka et al., 2009). Liu et al. (2012) reported that after Pb treatment, roots of *Ficus microcarpa* produced high concentrations of H₂O₂ along with an increase in O₂⁻ accumulation. O₂⁻ is produced by nicotinamide adenine dinucleotide phosphate (NADPH) oxidase in the plasma membrane, and is converted to H₂O₂ through non-enzymatic pathways or by superoxide dismutase (SOD; Passardi et al., 2004). Some ROS can alter gene expression and modulate the activity of specific proteins in the plant defense system (Sharma and Dubey, 2003). To protect cells and tissues from injury and dysfunction, plants have developed various strategies, such as over expression of SOD, catalase (CAT), peroxidase (POX), and ascorbate POX genes. In addition, non-enzymatic antioxidants with low molecular weights, such as proline, cysteine, non-protein thiol, ascorbic acid, and glutathione, which can reduce oxidative stress by scavenging ROS are synthesized (Choudhury and Panda, 2005; Singh et al., 2006; Malecka et al., 2009). Responses to metal toxicity involving these enzymes and non-enzymatic
antioxidants differ depending on the plant species, type of tissue, and metal concerned. Huang and Huang (2008) showed that in rice roots, Pb2+ induced ROS production and Ca2+ accumulation and activated MAP (mitogen-activated protein) kinases (proteins kinase cascade and major pathways by which extracellular stimuli are transduced into intracellular responses in all eukaryotic cells; Jonak et al., 2002) which are located in the apical region in rice roots. They demonstrated that treatment with glutathione, a powerful antioxidant, decreased Pb2+ induced root cells death and reduced MAP kinase activity. An increase in H2O2 content upon Pb exposure was observed in response to Pb2+, with an increase in CAT activity in Triticum aestivum (Kaur et al., 2013), Elsholtzia argyi (Islam et al., 2007), and Pisum sativum (Malecka et al., 2009). Pb-induced lipid peroxidation and enhanced H2O2 content in roots of Allium sativum (Liu et al., 2009), Z. mays (Gupta et al., 2009), and B. campestris (Singh et al., 2011). However, Islam et al. (2007) and Kaur et al. (2013) reported a decline in the activity of POXs in Elsholtzia argyi and Triticum aestivum roots upon Pb exposure. Therefore, a higher concentration of Pb or longer treatment inhibit cell metabolism and H2O2 production, resulting in a decrease in the activity of some antioxidant enzymes (CAT; Verma et al., 2003; Malecka et al., 2009). Plant enzymatic antioxidant defense systems vary with the plant species and with the intensity of Pb treatment. Production of ROS is common to different plant species. Some of these produced ROS may function as important signaling molecules by altering gene expression and modulating activity of specific defense proteins. However, ROS can be very harmful to organisms at high concentrations.

Lead also increased protein and proline contents in roots of two varieties of Z. mays with an increase in the concentration of Pb in the nutrient solution (Gohari et al., 2012). Proline plays an essential role in reducing environmental stress, including that caused by heavy metals. Pichalak et al. (2002) found that V. faba and Pisum sativum roots produced high amount of thiodipeptides and PCs after Pb exposure. Although, the high level of these proteins allows tolerance to Pb for these species roots.

CONCLUSION
Rost system is the first organ in contact with the different components of the soil and water. By their exudates and their effects on rhizosphere activities (proliferation of microorganisms, metal chelation, acidification, etc.) plant roots can tolerate and in some cases accumulate high levels of Pb. An overall higher rate of accumulation was observed in roots rather than leaves in several species. Almost 90% of Pb accumulated in a number of species of the Brassicaceae family (Kumar et al., 1995) and some crops species such as Z. mays (Malkowskii et al., 2002) and Pistia stratiotes (Vesely et al., 2012) was located in roots. This accumulator potential can be used in phytoammendment process. Rhizofiltration is a subset technique that uses both terrestrial and aquatic plants roots to absorb, concentrate, and precipitate metals from polluted water to their biomass (Dushenkov et al., 1995). This technique is cost-effective, and can be used for site restoration including maintenance of the biological activities of the polluted site. In this context, several plants have been identified whose roots could be used to clean up land contaminated by Pb. Therefore, improvement of the capacity of plant roots to tolerate and accumulate Pb by genetic engineering should open up new opportunities for rhizoamendment.

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