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ORIGINAL ARTICLE

Selection and characterization of lead-tolerant sweetpotato cultivars for phytoremediation

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Abstract
Lead (Pb) is one of the most toxic heavy metals (HMs) for plants and the environment. Sweetpotato [*Ipomoea batatas* (L.) Lam], the sixth most important food crop in the world, is tolerant to various environmental stresses, owing to its high antioxidant capacity. In this study, we selected sweetpotato cultivars showing high tolerance to lead (Pb) for phytoremediation-related applications. Young seedlings of 20 sweetpotato cultivars were treated with 30 mM Pb. Daeyumi (KO-12) and Dahomi (KO-5) were selected as Pb-tolerant and -sensitive cultivars, respectively, based on their photosynthetic activity and growth inhibition index (I_{50}). In the Pb treatment, hydrogen peroxide and malondialdehyde contents of KO-12 were 1.5-fold less than those of KO-5. In addition, KO-12 showed a higher ability to accumulate Pb in roots and leaves than KO-5. Expression levels of four Pb-responsive genes, including the metallothionein gene *IbMT1*, were higher in the roots and leaves of KO-12 than in those of KO-5. Interestingly, KO-12 showed greater tolerance to high Pb concentrations than sunflower and rapeseed, which have been well-studied for phytoremediation. Our results suggest that sweetpotato is a suitable biomaterial for the phytoremediation of soils contaminated with HMs, including lead, for sustainable agriculture.

Keywords Lead (Pb) · Sweetpotato · Phytoremediation · Heavy metals · Gene expression

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Abbreviations

HMs	Heavy metals
MDA	Malondialdehyde
qRT-PCR	Quantitative real-time polymerase chain reaction
ROS	Reactive oxygen species
TBA	Thiobarbituric acid
TCA	Trichloroacetic acid
MTs	Metallothioneins

Introduction

Heavy metal (HM) pollution is one of the major environmental problems worldwide (Mitra et al. 2022), and lead (Pb) is one of the most dangerous HMs. Pb pollution of air, water, and agricultural fields has adverse impacts on human health and the environment (Kshyanaprava and Das 2023; Sevak et al. 2021). The main sources of Pb-based environmental pollution include Pb ore mining and smelting, industrial effluents, fertilizers, pesticides, and municipal sewage sludge (Kushwaha et al. 2018).

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Several methods are currently available for cleaning the HM-contaminated soils and can be divided mainly into two categories: physicochemical and biological (Zhambakin and Zhapar 2020). The use of physicochemical methods of soil cleaning involves washing and chemical oxidation and reduction, which often leads to the accumulation of secondary pollutants and requires additional manipulations associated with the removal of contaminated soil cover and subsequent waste collection. The biological methods of soil decontamination involve phytoremediation, i.e., remediation of soil using live plants (Daurov et al. 2023). Phytoremediation is a promising technology that interacts harmoniously with the ecosystem (Mocek-Płóciniak et al. 2023), does not require expensive equipment, and is suitable for the elimination of a wide range of environmental pollutants. Moreover, the use of phytoremediation does not lead to the loss of soil fertility. Hyperaccumulator plants represent a valuable resource for the remediation of metal-contaminated sites as they can carry, absorb, and translocate high levels of HMs that would be toxic to most organisms.

In plants, Pb affects several metabolic processes in various subcellular compartments. Pb toxicity decreases seed germination, plant growth, and root and shoots dry biomass, violates mineral nutrition (Sharma and Dubey 2005), reduces cell division, and inhibits photosynthesis (Nas and Ali 2018). The study of plant responses to external factors reveals the physiological and biochemical mechanisms and adaptation limits of plants (Sapakhova et al. 2023). In addition, Pb has been reported to produce reactive oxygen species (ROS) and increase antioxidant enzyme activity in plants (Samuel et al. 2022). The ROS generated as a result of oxidative stress have various harmful effects on plant cells, such as inhibition of photosynthetic activity, inhibition of adenosine triphosphate (ATP) production, and lipid peroxidation (Pourrut et al. 2011). One of the main consequences of accumulating Pb is the increased production of ROS, which damages cell membranes, nucleic acids, and chloroplast pigments (Afaj et al. 2017; Nas and Ali 2018). Moreover, key members of the peroxidase (POD) family play a critical role in the enzymatic removal of ROS, thus protecting plant cells from oxidative stress (Gülen et al. 2008). Pb toxicity accelerates the production of ROS including hydrogen peroxide (H_2O_2), which, in turn, causes secondary oxidative stress, leading to growth inhibition at the seedling stage (Yang et al. 2010). When plants encounter extreme levels of environmental stress, their malondialdehyde (MDA) levels increase (depending on the nature of the stress). The content of MDA represents the level of lipid peroxidation, and an elevated MDA level indicates stress. In rice, high concentrations of Pb significantly reduced plant yield, adversely affected various biochemical and physiological processes (Xie et al. 2018), and increased the antioxidant level (Mandiwana et al. 2007). These studies show that strengthening the antioxidant defense system helps plants to overcome HM-induced stress.

The study of gene expression in plants is receiving increasing attention from researchers around the world (Hieno et al. 2019). As with other stress factors, numerous protective genes are expressed when exposed to heavy metals. Abiotic factors, including heavy metals, are the most common stress factors that negatively affect plant growth and development. Plants respond to stress factors at the molecular, cellular and physiological levels through various perceptions and transduction of stress signals, which subsequently activate a variety of defense mechanisms (Rejeb et al. 2014). Recently, there has been great interest in studying the expression of the metallothionein (*MT*) gene, which plays an important role in heavy metal tolerance in plants (Kim et al. 2010, 2014; Sung et al. 2019). MTs, low-molecular-weight proteins (7–10 kDa) with a high percentage of cysteine (Cys) residues (Bourdineaud et al. 2006; Cobbett and Goldsbrough 2002; Pan et al. 2018), have been widely characterized in various prokaryotic and eukaryotic organisms. Plant MTs are classified into four types according to the arrangement of their Cys residues (Robinson et al. 1993), including the *MT1*, *MT2*, *MT3*, and *MT4* subfamilies (Cobbett and Goldsbrough 2002; Leszczyszyn et al. 2013). MTs play crucial roles in ion homeostasis and tolerance in plants. The *HMA3* gene plays an important role in the transport and regulation of various metals, including lead, zinc, cobalt and other heavy metals (Takahashi et al. 2012; Williams and Mills 2005). Heavy-metal-associated proteins (HMAs) have been extensively studied at the molecular level in *Arabidopsis thaliana* and *Oryza sativa*, where eight and nine *HMA* genes (*AtHMAs* and *OsHMAs*) were discovered, respectively (Takahashi et al. 2012; Williams and Mills 2005). There is also widespread interest in studying the expression of genes encoding peroxidase (*swpb3* and *swpa4*) (Jang et al. 2004; Kim et al. 2010), which have a key role in the oxidation of molecules when exposed to heavy metals in plants.

Sweetpotato [*Ipomoea batatas* (L.) Lam] is an emerging root crop with the potential to ensure global food and nutrition security in the face of the climate crisis (Kwak 2019). Sweetpotato was evaluated as one of 10 superfoods for better health since it contains high levels of low-molecular-weight antioxidants, dietary fiber, minerals including potassium as well as large amounts of carbohydrates (Alam et al. 2020; CSPI 2007; Sun et al. 2019). In the field, sweetpotato plants show high tolerance to environmental stresses including drought and high temperature, owing to their high antioxidant activity (Chauhan et al. 2021; Chen et al. 2016; Wang et al. 2019; Yang et al. 2020). In addition, sweetpotato serves as a cover crop and root crop, reducing soil erosion in the rainy season. Thus, sweetpotato has many characteristics suitable for the phytoremediation of HM-contaminated soils.

Few studies have been conducted to study the phytoremediation capacity of sweetpotatoes on HM-contaminated soil (Izinyon and Seghosime 2013; Kim et al. 2010, 2014; Tamungang et al. 2016). In addition, the antioxidant protection of sweetpotatoes against the toxic effects of ROS under Pb stress has not been sufficiently explained. Thus, this study aimed to investigate the potential of sweetpotatoes as a remediation plant for Pb-contaminated soil.

Materials and methods

Plant materials and growth conditions

Twenty Korean sweetpotato cultivars were used in this study: Daeyumi (KO-12), Dahomi (KO-5), Danjami, Geonhwangmi (KO-7), Hogammi, Jammi, Jeonmi, Jinhongmi, Jinmi, Jinyulmi, Matnami (KO-16), Pungwonmi, Saengmi, Shingunmi, Shinzami, Shinyulmi, Yesmi, Yeonhwangmi, Yeonmi, and Yulmi. These cultivars were obtained from the Bioenergy Crop Research Institute, National Institute of Crop Science, Rural Development Administration, Muan, Korea. Each plant was placed in a square tray (40 cm × 16 cm × 13 cm) and grown at 25 °C under 16 h/8 h light/dark cycle and 50% relative humidity. Stem cuttings were prepared from young seedlings as described previously (Park et al. 2020).

Pb treatments

To select sweetpotato cultivars with high tolerance to Pb, 10-day-old seedlings of 20 sweetpotato cultivars were treated with 300 mL of water containing 30 mM $Pb(NO_3)_2$ for 2 weeks. Plant phenotypes of each sweetpotato cultivar were evaluated and scored on a scale of 0 (complete damage) to 10 (no damage), according to leaf damage by Pb stress. To compare the 50% inhibition (I_{50}) concentrations of Pb between two Pb-tolerant cultivars (KO-12 and KO-16) and two Pb-sensitive cultivars (KO-7 and KO-5), 14-day-old seedlings were treated with different concentrations of Pb (0, 1, 5, 10, 15, and 30 mM) for 30 days. After 30 days of Pb treatment, the leaves and roots of plants were separated and weighed to determine their fresh weight. To compare the phytoremediation capacity of sweetpotato with that of other crops, young plants of sunflower and rapeseed cultivars were treated with Pb (as described above) for 2 weeks. All experiments were carried out in a randomized complete block design with four replications.

Photosynthetic activity and chlorophyll content measurements

Chlorophyll contents and photosynthetic activity were measured in the second and third leaves (from the top) of two Pb-tolerant and two Pb-sensitive cultivars at 2 weeks after Pb treatments (0, 1, 5, 10 mM). To measure photosynthetic activity, the photochemical yield (Fv/Fm) of leaves was determined using a portable chlorophyll fluorometer (HANSATECH, Serial Number 1947, England) after 30 min of dark adaptation. The chlorophyll content of leaves was measured using a portable chlorophyll meter (Junior-PAM Chlorophyll Fluorometer; Heinz Walz, Germany).

MDA and H_2O_2 quantification

The leaves and roots of Pb-treated plants were separated and immediately frozen in liquid nitrogen. The content of MDA, which indicates the level of lipid peroxidation, was measured using the modified thiobarbituric acid (TBA) method (Wang et al. 2009). Root extracts were assayed with 20% trichloroacetic acid (TCA) and 0.5% TBA, and the absorbance of extracts was quantified at 532 and 600 nm. The H_2O_2 content was measured using the potassium iodide method (Junglee et al. 2014), and the absorbance of extracts was recorded at 390 nm. Samples were extracted using 0.1% TCA extraction buffer in both assays. The samples were homogenized with extraction buffer and centrifuged for 5 min.

Quantification of Pb in plant tissues

To measure the content of Pb content in plant tissues, young seedlings of KO-12 (Pb tolerant) and KO-5 (Pb sensitive) cultivars were treated with 10 mM Pb for 10 days. Leaves and roots of the harvested plants were dried in an oven at 60 °C. First, 25 mL of HNO_3 was added to 0.1 g (dry weight) of the plant sample. The sample was left stationary for 24 h and then decomposed by heating at 120 °C for 2 h using a heating block. Pb content was determined using a flame atomic absorption spectrophotometer, equipped with a hollow cathode lamp and an air-acetylene flame (AnalytikJena AG, novAA 350, Jena, Germany), at 283.3 nm wavelength (Toishimanov et al. 2023).

Gene expression analysis

The leaves and roots of KO-12 and KO-5 plants treated with 20 mM Pb were harvested at 0.5, 1, and 3 days after treatment (DAT). Total RNA was extracted from the leaf and root samples using TRI Reagent (Molecular Research Center, USA, TR 118), according to the manufacturer's protocol. To remove genomic DNA contamination, the total RNA was treated with RNase-free DNase I (Thermo Fisher Scientific, USA). The purity and quantity of DNase I-treated total RNA were confirmed using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA). First-strand cDNA synthesis was conducted in a 13-μL reaction mixture containing 0.1 ng to 5 μg of total RNA and 0.6 μg (100 pmol) of oligo(dT)$_{18}$ primer (Thermo Scientific RevertAid Reverse Transcriptase), according to the manufacturer's instructions. The mixture was incubated at 65 °C for 5 min. Then, a 7-µL reaction mixture was prepared that contained 4 µL of 5 × reverse transcription reaction buffer, 2 µL of 10 mM dNTP mix, and 1 µL (200 units) of Moloney Murine Leukemia Virus (M-MuLV) reverse transcriptase. The mixture was incubated at 42 °C for 60 min, followed by a reaction stop by heating the mixture at 70 °C for 10 min.

The expression levels of four Pb-responsive genes encoding metallothionein (*IbMT1*), ATPase 3 homolog (*IbHMA3*), and two PODs (*swpb3* and *swpa4*) (Kim et al. 2010, 2014) by measured by quantitative real-time PCR (qRT-PCR). The qRT-PCR was performed on the CFX Connect™ Real-Time System (Bio-Rad, Hercules, CA, USA) using EvaGreen fluorescent dye and gene-specific primers (Supplemental Table 1) under the following conditions: initial denaturation at 95 °C for 15 min, followed by 40 cycles of denaturation at 95 °C for 20 s, annealing at 58 °C for 40 s, and extension at 72 °C for 20 s. The melting curves were verified to confirm primer specificity. The ubiquitin (*UBI*) gene was used as an internal reference, and relative gene expression was quantified using the $2^{-\Delta\Delta CT}$ method.

Statistical analysis

One-way analysis of variance (ANOVA) was conducted to identify statistically significant differences ($p < 0.05$). Tukey's honestly significant difference (HSD) post-hoc test was used to perform multiple pairwise comparisons. Principal component analysis (PCA) was completed using the fviz-pca function of the factoextra R package Ver. 1.0.7 in RStudio. Pearson's correlation analysis was completed using the mcor function, and corrplots were prepared using the corrplot package Ver. 0.92 in RStudio.

Results

Selection of Pb-tolerant and -sensitive sweetpotato cultivars

To select sweetpotato cultivars with high Pb tolerance, the appropriate Pb concentration was determined using the Yulmi cultivar (KO-1). Ten-day-old seedlings were treated with 300 mL of water containing different concentrations of Pb (0, 20, 30, 50, and 100 mM $Pb(NO_3)_2$) for 2 weeks. The sweetpotato seedlings showed leaf damage in a Pb dosage-dependent manner (Fig. 1). No obvious damage to leaves was observed in the 20-mM Pb treatment for 2 weeks, but clear leaf damage was evident in the 30-mM Pb treatment after 1 week. Seedlings treated with high Pb concentrations (50 and 100 mM) showed severe damage from one week onward. Thus, we determined 30 mM as the optimal Pb concentration for evaluating the Pb tolerance of 20 sweetpotato cultivars.

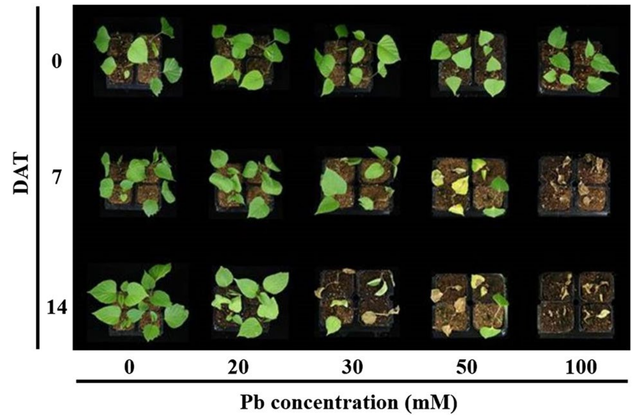

Fig. 1 Phenotypic evaluation of the sweetpotato cultivar Yulmi treated with various Pb concentrations for 14 days. *DAT* days after treatment

Table 1 Evaluation of the Pb tolerance of 20 sweetpotato cultivars based on leaf damage

Cultivar	Score†	Cultivar	Score†
KO-1 (Yulmi)	1	KO-19 (Saengmi)	7
KO-3 (Shinjami)	8	KO-20 (Shingunmi)	3
KO-4 (Pungwonmi)	8	KO-21 (Yeonmi)	5
KO-5 (Dahomi)	1	KO-22 (Yesmi)	2
KO-7 (Geonhwangmi)	1	KO-23 (Jammi)	5
KO-10 (Shinyulmi)	2	KO-24 (Jeonmi)	7
KO-11 (Yeonhwangmi)	7	KO-27 (Jinmi)	8
KO-12 (Daeyumi)	10	KO-28 (Jinyulmi)	3
KO-15 (Danjami)	3	KO-29 (Jinhongmi)	5
KO-16 (Matnami)	9	KO-32 (Hogammi)	6

†Leaf damage caused by 14-day exposure to 30 mM Pb was scored on a scale from 0 (complete damage) to 10 (no damage)

To select sweetpotato cultivars with high tolerance to Pb, 10-day-old seedlings of 20 cultivars were treated with 30 mM of $Pb(NO_3)_2$ for 14 days. Even though seedlings of all cultivars survived in the 30-mM Pb treatment, differences in leaf phenotypes were observed among the 20 cultivars. The Pb-induced leaf damage was scored on a scale of 0–10 for each cultivar (Table 1). Daeyumi (KO-12) was the most Pb-tolerant cultivar. Matnami (KO-16), KO-4 (Pungwonmi), and KO-27 (Jinmi) also showed high Pb tolerance. However, Dahomi (KO-5), and Geonhwangmi (KO-7) were the most sensitive to Pb. Sensitive cultivars clearly showed leaf chlorosis, stunting, and yellowing (data not shown). Thus, based on plant phenotypes, we tentatively determined KO-12 and KO-16 as two Pb-tolerant cultivars and KO-7 and KO-5 as two Pb-sensitive cultivars and characterized them further.

To confirm the phenotypic responses of Pb-tolerant (KO-12 and KO-16) and Pb-sensitive (KO-7 and KO-5) cultivars to Pb exposure, young seedlings were treated with various Pb concentrations (0, 1, 5, 10, 15, and 30 mM) for 30 days. All four cultivars showed clear phenotypic differences at different Pb concentrations (Fig. 2A). The severity of leaf damage in each cultivar and the degree of phenotypic differences among cultivars increased with the increase in Pb concentration and treatment time. KO-12 seedlings appeared quite healthy on day 5 in the 30-mM Pb treatment, whereas KO-5 seedlings showed severe leaf damage on day 1 in the 20-mM Pb treatment. Plant growth was analyzed by measuring the leaf fresh weight of all four cultivars treated with Pb for 30 days (Fig. 2B). The I_{50} values, calculated on the basis of leaf fresh weight, were 6.7, 3.2, 2.0, and 1.3 mM for KO-12, KO-16, KO-7, and KO-5, respectively. The I_{50} value of KO-12 (6.7 mM) was 5.1 times higher than that of KO-5 (1.3 mM). Therefore, based on the I_{50} value, we designated KO-12 as the most Pb-tolerant sweetpotato cultivar.

Chlorophyll content and photosynthetic activity

To compare the physiological responses of Pb-tolerant (KO-12 and KO-16) and Pb-sensitive (KO-7 and KO-5) cultivars, the chlorophyll content and photosynthetic activity of plants treated with Pb (0, 1, 5, 10 mM) for 15 days were analyzed (Fig. 3A, B). Both the chlorophyll content and photosynthetic activity of sweetpotato cultivars decreased significantly with the increase in Pb concentration. KO-12 (the most Pb-tolerant cultivar) showed a stable chlorophyll content. However, in the 10-mM Pb treatment, chlorophyll contents of KO-16, KO-7, and KO-5 were 1.3-, 1.4-, and 1.7-fold lower than that of KO-12, respectively. Additionally, the photosynthetic activity (Fv/Fm) of KO-12 was 1.2-,

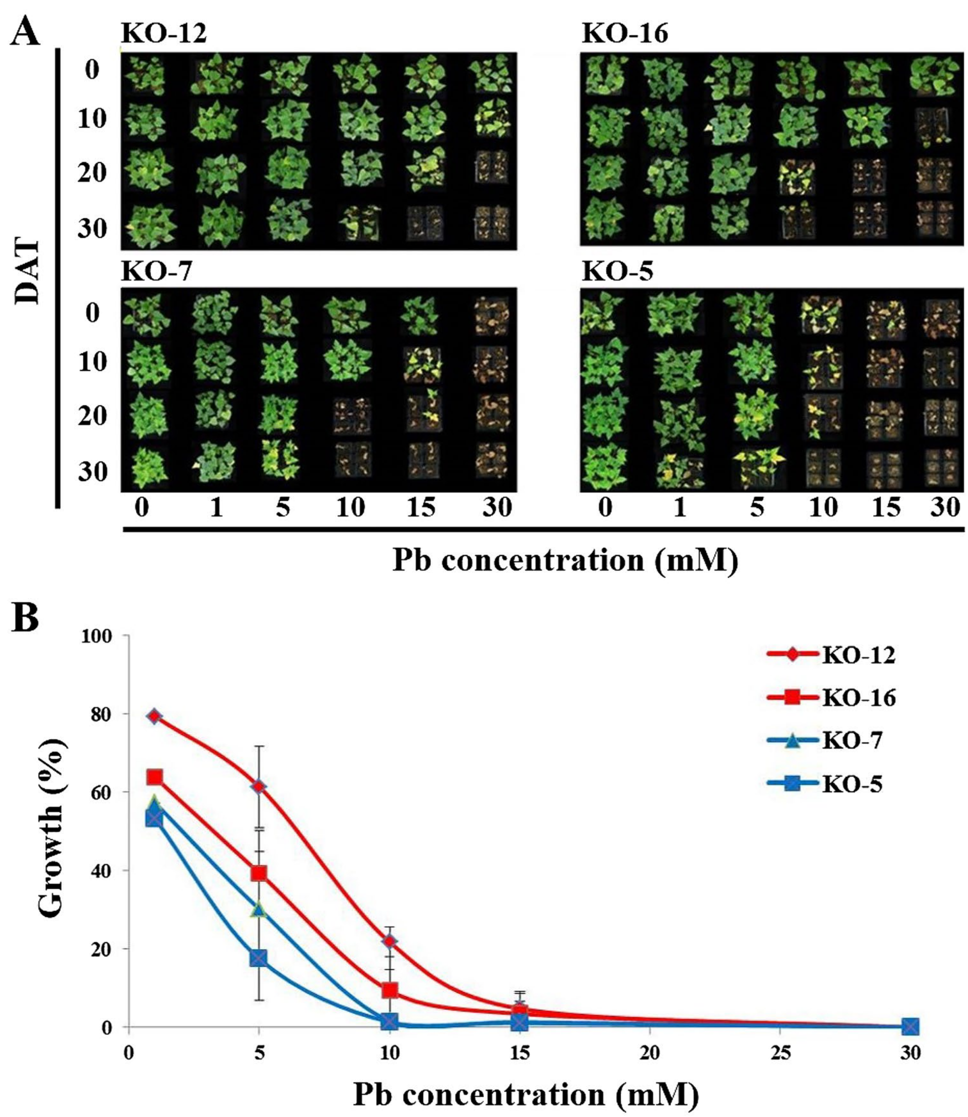

Fig. 2 Phenotypic and growth analyses of two Pb-tolerant and two Pb-sensitive sweetpotato cultivars treated with various concentrations of Pb for 30 days. **A** Plant phenotypes. **B** Relative plant growth determined on the basis of leaf fresh weight (%). Data represent mean ± SD of four independent replicates. Red line, Pb-tolerant cultivars; blue line, Pb-sensitive cultivars; *DAT* days after treatment

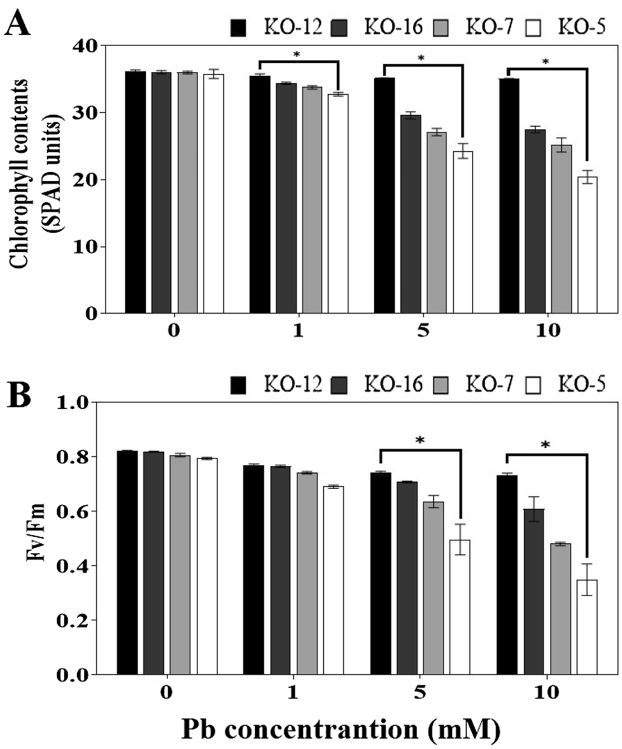

Fig. 3 Physiological analysis of four sweetpotato cultivars treated with different concentrations of Pb stress for 15 days. **A** Chlorophyll contents of leaves (SPAD unit); **B** photosystem II efficiency (Fv/Fm). Data represent mean ± SD of four independent replicates. Asterisks indicate significant differences among cultivars (*$p < 0.05$; one-way analysis of variance [ANOVA] with Tukey's HSD post-hoc test)

1.5-, and 2.1-fold times higher than that of KO-16, KO-7, and KO-5, respectively, in the 10-mM Pb treatment. These results confirmed that KO-12 exhibits higher chlorophyll content and greater photosynthetic activity than the other sweetpotato cultivars, owing to its high Pb tolerance.

MDA and H_2O_2 contents

In the 10-mM Pb treatment, the MDA content of roots started to show a significant difference between KO-12 and KO-5 cultivars from day 1 (Fig. 4). At 10 DAT, the MDA content of KO-5 roots was approximately 1.4-fold higher than that of KO-12 roots. Similarly, the MDA content of leaves started showing a significant difference between KO-12 and KO-5 cultivars from day 5 onward. At 10 DAT, the MDA content of KO-5 leaves was approximately 1.3-fold higher than that of KO-12 leaves.

The H_2O_2 content of KO-5 and KO-12 roots sharply increased from day 3 onward. At 5 and 10 DAT, the H_2O_2 content of KO-5 leaves was approximately 1.2- and 1.5-fold higher than that of KO-12 leaves, respectively. These results indicate that KO-12 exhibits high antioxidant activity to cope with Pb-induced oxidative stress.

Pb accumulation in different tissues

Figure 5 shows that sweetpotato plants accumulate Pb in both roots and leaves. The Pb content of roots of both KO-12 and KO-5 cultivars started increasing from day 1 onward. At 10 DAT, Pb content of KO-12 roots (4600 mg/kg) was approximately 1.2-fold higher than that of KO-5 roots (3797 mg/kg). Once absorbed by the roots, Pb is translocated to leaf tissues. The leaves of KO-12 also accumulated high levels of Pb compared with those of KO-5; at 10 DAT, the level of Pb accumulation in KO-12 leaves (507 mg/kg) was approximately 2.0-fold higher than that in KO-5 leaves (251 mg/kg). These results indicate that the Pb-tolerant KO-12 cultivar can efficiently absorb Pb through the roots and translocate it to leaf tissues.

Expression analysis of Pb-responsive genes

To understand the differences between the Pb-tolerant KO-12 and Pb-sensitive KO-5 cultivars at the molecular level, we examined the expression of four genes involved in HM tolerance in sweetpotato: *IbMT1* (encoding metallothionein), *IbHMA3* (encoding ATPase3 homolog), and *swpb3* and *swpa4* (encoding PODs). All four genes showed differences in expression patterns between the two cultivars (Fig. 6). Pb-tolerant KO-12 showed higher expression levels of the four genes in both leaves and roots than Pb-sensitive KO-5. The expression of IbMT1 started increasing in both the leaves and roots of KO-12 at 12 h after the Pb treatment. Compared with the KO-5 cultivar, KO-12 showed a significantly higher expression level of *IbHMA3* at 1 DAT in leaves and at 0.5 DAT in roots. The expression levels of *swpb3* and *swpa4* were higher in KO-12 than in KO-5. The *swpb3* gene was highly expressed in the leaves of both KO-12 and KO-5 cultivars at 0.5 DAT and thereafter; however, in the roots of both cultivars, *swpb3* showed a similar level regardless of the Pb treatment duration. The *swpb4* gene showed higher expression in both the leaves and roots of KO-12 than in those of KO-5 starting at 0.5 DAT. In the leaves and roots of the KO-12 cultivar, *swpb4* showed the highest expression level at 1 and 3 DAT, respectively. Our results confirmed that the Pb-tolerant KO-12 cultivar has a Pb tolerance mechanism at the molecular level.

Principal component analysis and correlation analysis

To assess the impact of Pb treatment on tolerant and sensitive cultivars of sweetpotato, PCA was used for multidimensional analysis. The variables that exist closely and in the same quadrant are positively correlated. The first two components, such as PC1 (87.8%) and PC2 (8.4%), made the most significant contribution, constituting 96.2% of

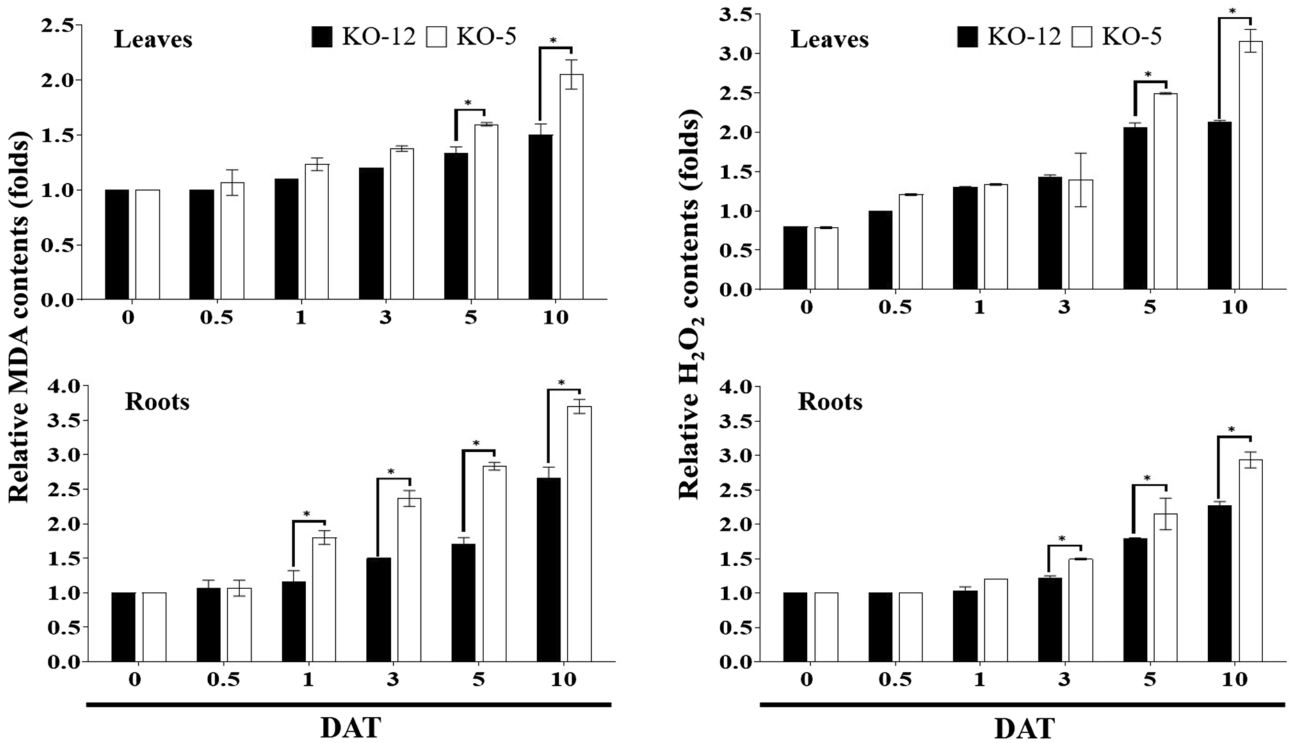

Fig. 4 Relative malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) contents of the leaves and roots of KO-12 (Pb-tolerant) and KO-5 (Pb-sensitive) cultivars. Data represent mean ± SD of four independent replicates. Asterisks indicate significant differences among cultivars (*$p < 0.05$; ANOVA with Tukey's HSD post-hoc test). *DAT* Days after treatment

the total variance among physiological and biochemical parameters, thereby confirming the trend of the results (Supplemental Fig. 1A). This segregation of treatments indicates that Pb treatment had a significant enhancing effect on the physiological and biochemical parameters of sweetpotato. Pb treatment at high concentrations showed a strong positive correlation with MDA and H_2O_2. Conversely, a notable negative correlation of PC1 variables comprised photosynthetic activity and chlorophyll, which are associated with PC2 (Supplemental Fig. 1B). Pearson's correlation analysis was conducted among tolerant and sensitive varieties of sweetpotato (Supplemental Fig. 1C). The correlation analysis revealed that physiological indicators (Pn and Chl) positively correlated with each other; in the meantime, there were negatively correlated with biochemical parameters MDA and H_2O_2 (Supplemental Fig. 1C). Similarly, the concentration of Pb in roots and leaves also demonstrated a negative correlation of biochemical parameters with plant physiological parameters, indicating a close connection between Pb concentrations and physiological parameters, and the resilience of sweetpotato to Pb.

Comparison of the Pb tolerance of sweetpotato, sunflower, and rapeseed

We compared the phytoremediation capacity of sweetpotato cultivar KO-12 with that of rapeseed and sunflower, which have been well-studied for the clean-up of HM-contaminated soils (Eapen and Dsouza 2005; Eapen et al. 2007; Prasad 2015). Young rapeseed and sunflower plants at a similar growth stage as sweetpotato (KO-12) plants were treated with $Pb(NO_3)_2$ for 14 days as described above. Rapeseed and sunflower plants died at 30 mM Pb, whereas sweetpotato plants survived both 30 and 50 mM Pb treatments (Supplemental Fig. 2A). To perform a quantitative comparison among the three plant species, the I_{50} value of each plant species was calculated based on plant growth at different Pb concentrations (Supplemental Fig. 2B). The I_{50} values of sweetpotato, sunflower, and rapeseed were 9.5, 7.3, and 6.2 mM Pb, respectively. Thus, sweetpotato shows high potential as a suitable root crop for the phytoremediation of soils contaminated with Pb and possibly other HMs.

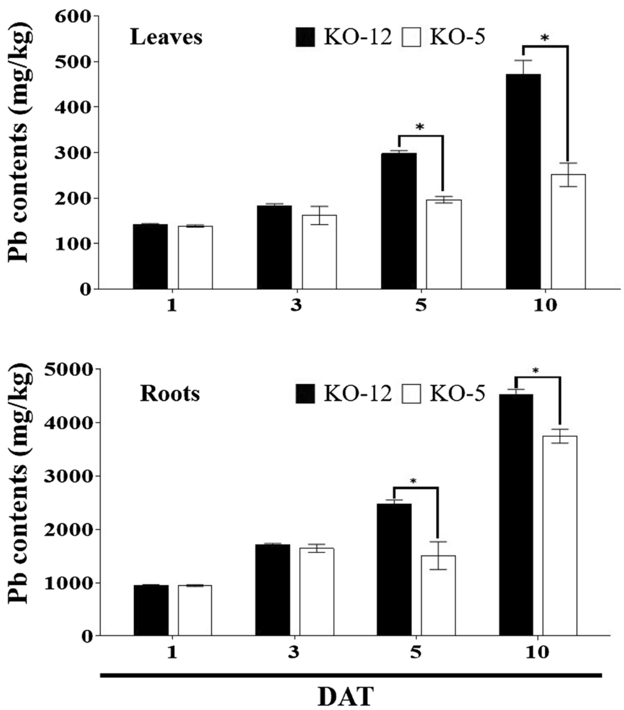

Fig. 5 Pb contents of the leaves and roots of KO-12 and KO-5 cultivars treated with 10 mM Pb. Data represent mean ± SD of four independent replicates. Asterisks indicate significant differences among cultivars at a given time point (*$p < 0.05$; one-way ANOVA with Tukey's HSD post-hoc test). *DAT* Days after treatment

Discussion

Sweetpotato offers many advantages over other starchy crops on marginal lands, including HM-contaminated soils, for sustainable agriculture (Mohammad 2021; Mohanraj 2018; Ziska et al. 2009). Moreover, sweetpotato shows high water use efficiency and reduce soil erosion during the rainy season, and therefore can be used as a cover crop. The minimum requirement for sweetpotato cultivation is a frost-free period lasting at least 4 months.

A high concentration of HMs such as Pb can cause a number of toxic symptoms in plants, such as growth retardation (stunting), poor photosynthesis (chlorosis), and root blackening. Pb can inhibit photosynthesis, disrupt mineral nutrition and water balance, and affect membrane structure and permeability (Nas and Ali 2018).

According to our scientific knowledge, sweetpotato, a root crop, can be suitable for phytoremediation, because its high antioxidant activity can help cope with oxidative stress caused by HMs. Although the presence of HMs in sweetpotato storage roots has been investigated in terms of food safety (Zhang et al. 2018), an intensive analysis of sweetpotato plants for phytoremediation is lacking. In this study, we screened the responses of 20 sweetpotato cultivars to Pb treatment with the aim to identify cultivars with high Pb tolerance. Finally, we selected two Pb-tolerant cultivars (KO-12 and KO-16) and two Pb-sensitive cultivars (KO-7 and KO-5) for further analysis (Table 1). In our experiments, as the Pb concentration and the treatment time increased, the total biomass of plants decreased (Fig. 2B). A similar result has previously been reported in other plant species upon Pb exposure (Zulfiqar et al. 2019).

Among the various physiological processes that determine plant growth and productivity, photosynthesis is the most important. The main reason for the decrease in the content of green pigments in plants under HM toxicity is the suppression of chlorophyll synthesis (Mukhtar et al. 2010; Nawaz et al. 2017). We confirmed that Pb-tolerant cultivars showed higher growth and greater photosynthetic activity than Pb-sensitive cultivars (Fig. 3). The Pb-tolerant cultivar KO-12, when treated with 10 mM for 10 days, showed more stable chlorophyll content and photosynthetic activity that the Pb-sensitive cultivar KO-5. A similar decrease in photosynthetic activity after exposure to HMs, including Pb, has been observed in other plant species (Giannakoula et al. 2021; Mukhtar et al. 2010). Moreover, it has been reported that changes in photosynthetic activity due to Pb exposure lead to decreased growth rate and total plant biomass (Beat et al. 2022).

Based on the obtained results, we can infer that elevated concentrations of Pb are potentially toxic to sweetpotatoes, with high concentrations leading to chlorosis and poor plant growth. Such a trend is observed in other studies investigating the effects of heavy metals on various plants (Dalyan et al. 2020; Zulfiqar et al. 2019). At the same time, some plant genotypes exhibit greater tolerance to different stress conditions compared to others. In our case, the Pb-tolerant cultivar of sweetpotato (KO-12) was able to grow and thrive under elevated lead concentrations in the soil and thus could potentially serve as a phytoremediant.

The I_{50} values were calculated for the Pb-tolerant cultivars KO-12 and KO-16 and Pb-sensitive cultivars KO-7 and KO-5 based on leaf fresh weight. The I_{50} value of KO-12 (6.7 mM) was 5.1 times higher than that of KO-5 (1.3 mM). We speculated that all sweetpotato cultivars exhibit relatively high tolerance to Pb stress, regardless of their genotype, because of their high antioxidant capacity (Kim et al. 2020). However, a comparison of the I_{50} values of the four cultivars indicated that the KO-12 cultivar is the most tolerant to Pb stress. Interestingly, our previous study showed that KO-12 is also highly tolerant to other HMs including cadmium, arsenic, copper, cobalt, and nickel.

Lipid peroxidation is a sign of oxidative stress caused by various abiotic stresses. MDA level is indicative of the level of lipid peroxidation, indicating that high MDA level reflects damage to cell membranes in plants (Morales and Munné-Bosch 2019). MDA has been well characterized as an evaluative trait of HM-stressed plants (Lamhamdi et al.

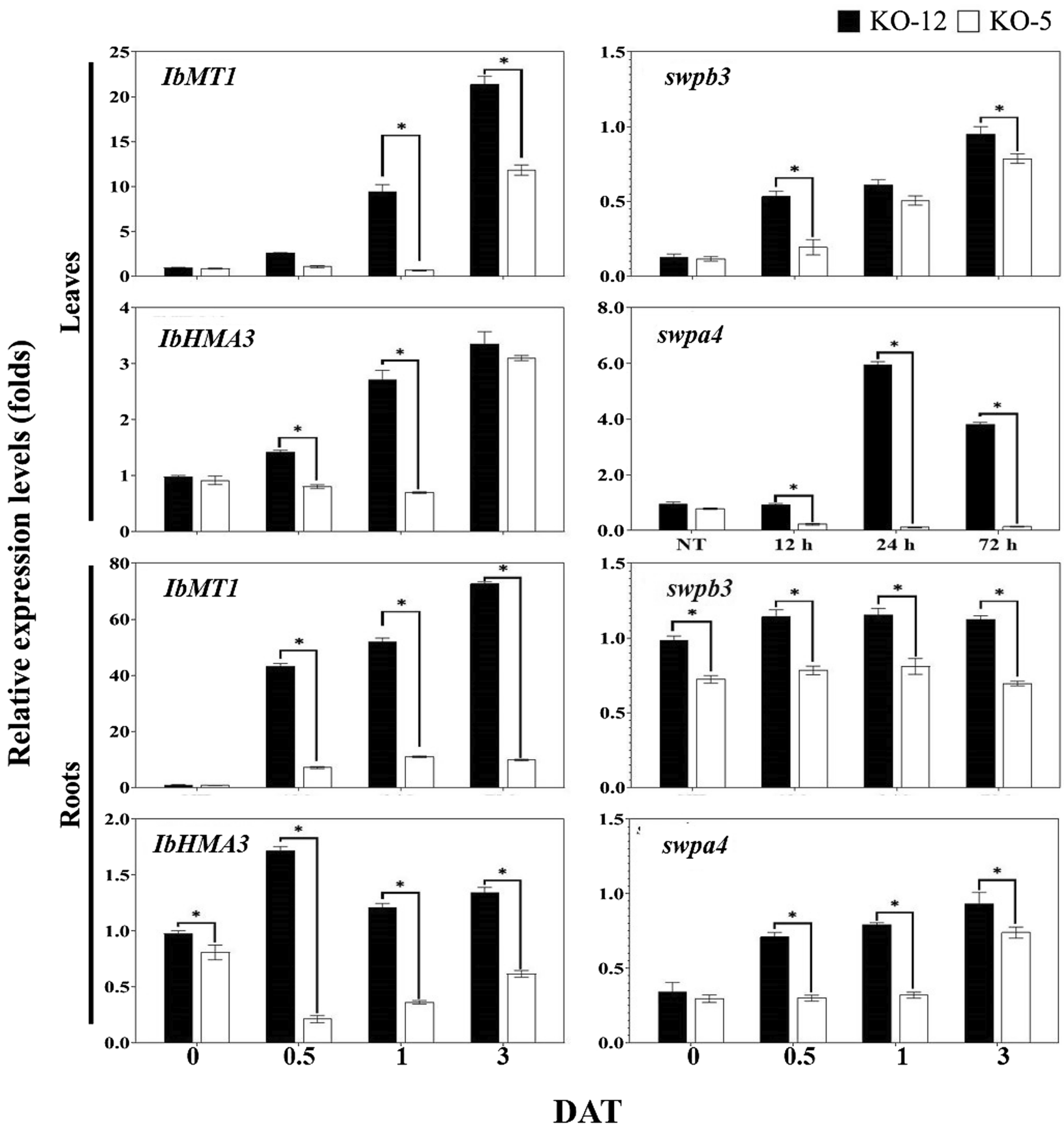

Fig. 6 Expression patterns of Pb-responsive genes in the leaves and roots of KO-12 and KO-5 cultivars treated with 20 mM Pb. Data represent mean ± SD of four independent replicates. Asterisks indicate significant differences among cultivars at a given time point (*$p < 0.05$; one-way ANOVA with Tukey's HSD post-hoc test). *DAT* Days after treatment

2013). The MDA content of the roots of KO-12 and KO-5 cultivars significantly increased from 1 day after Pb treatment (Fig. 4). At 10 DAT, the MDA contents of the roots and leaves of KO-5 were approximately 1.4 and 1.3 times higher, respectively, than those of KO-12. Previously published data show that exposure to Pb significantly increases the MDA content of plant cells (Navabpour et al. 2020).

The production of H_2O_2, the main ROS, increases under HM stress (Sachdev et al. 2021). At 5 and 10 DAT, the H_2O_2 content of KO-5 leaves was approximately 1.2 and 1.5 times higher, respectively, than that of KO-12 leaves, respectively. A significant increase in H_2O_2 levels in plants subjected to Pb exposure has also been reported previously (Navabpour et al. 2020). Our results indicate that the sweetpotato cultivar KO-5 exhibits high antioxidant activity to cope with Pb-induced oxidative stress.

To tackle the increased levels of environmental pollution, the ability of plants to accumulate HMs is important. Our results showed that sweetpotato plants can accumulate Pb in roots and leaves (Fig. 5). At 10 DAT, the Pb accumulation levels in KO-12 roots and leaves were approximately 1.2 and 2.0 times higher, respectively, than those in the corresponding KO-5 tissues. A recent study showed higher Pb accumulation in roots than in leaves (Souri et al. 2019).

To understand the differences between the KO-12 (Pb-tolerant) and KO-5 (Pb-sensitive) cultivars at the molecular level, the expression levels of four Pb-responsive genes (*IbMT1*, *IbHMA3*, *swpb3*, and *swpa4*) were analyzed. The expression levels of all four genes were higher in the leaves and roots of KO-12 than in those of KO-5 (Fig. 6). Metallothioneins (MTs) are low-molecular-weight proteins (7–10 kD). The sulfur-containing amino acid cysteine, whose sulfhydryl groups are capable of binding HM ions, accounts for approximately 30% of all amino acids in MTs. To date, four types of MT proteins have been identified (MT1, MT2, MT3, and MT4), which differ in the number and location of cysteine residues (Duan et al. 2019). The expression of *MT1* is more pronounced in plant roots than in stems and leaves. In our study, the *IbMT1* gene was highly expressed in the leaves and roots of KO-12 starting at 12 h in the Pb treatment. Similar work has also been carried out with the *MT* genes in other plant species, with similar results (Kim et al. 2014; Kim and Kang 2018; Nezhad et al. 2013).

The ATPase-related transport protein HMA3 transfers free HM ions through the tonoplast using the energy generated by ATP hydrolysis. In *Arabidopsis thaliana*, overexpression of the *AtHMA3* gene increased tolerance not only to Cd^{2+} but also to Co^{2+}, Pb^{2+}, and Zn^{2+} (Hermosa et al. 2011). In the current study, the expression level of *IbHMA3* in the KO-12 cultivar was highest at 1 DAT in leaves and at 0.5 DAT in roots. High-level expression of *HMA3* has been reported in the aerial tissues of *Sedum plumbizincicola* (Liu et al. 2017). In other crops, the high expression level of HMA3 in aerial plant parts and roots was associated with the hyperaccumulation of HMs (Talke et al. 2006; Ueno et al. 2011).

POD enzymes protect cells from HM-induced oxidative stress (Kim et al. 2010; Zhang et al. 2023). The expression levels of sweetpotato *POD* genes *swpb3* and *swpa4* have been reported to significantly increase in leaves and roots in response to HM treatment (Kim et al. 2010). Consistently, in our study, *swpb3* and *swpa4* showed higher expression levels in KO-12 than in KO-5. Our results confirmed that the Pb-tolerant KO-12 cultivar is equipped with a Pb tolerance mechanism at the molecular level. Further investigation of the molecular mechanism underlying HM tolerance in sweetpotato is needed for the molecular breeding of sweetpotato cultivars suitable for phytoremediation.

More than 450 hyperaccumulator plant species are currently used for soil remediation (Skuza et al. 2022). In this study, we compared the phytoremediation capacity of sweetpotato cultivar KO-12 with that of rapeseed and sunflower, which are well-studied for the clean-up of HM-contaminated soils (Eapen and Dsouza 2005; Eapen et al. 2007; Prasad 2015). Sweetpotato plants showed greater tolerance to Pb stress than rapeseed and sunflower plants (Supplemental Fig. 2). The I_{50} value of sweetpotato, sunflower, and rapeseed was 9.5, 7.3, and 6.2 mM Pb. These results suggest that sweetpotato is suitable for the remediation of HM-contaminated soils.

We also compared the Pb tolerance of sweetpotato, sunflower, and rapeseed and analyzed their plant growth inhibition indexes under high Pb concentrations. The results showed that sweetpotato is more tolerant to Pb toxicity than sunflower and rapeseed. Additionally, the plant growth inhibition index of sunflower and rapeseed was 1.3 and 1.5 times higher than that of sweetpotato (Supplemental Fig. 2A, B). The results indicate that sweetpotato is highly Pb tolerant and therefore an excellent candidate for the remediation of HM-contaminated soils. Moreover, sweetpotato storage roots produced on HM-contaminated soils can be used for the extraction of useful biomaterials including bioethanol Ziska et al. 2009). In this study, the results of physiological, biochemical, and molecular analyses suggest that Pb-tolerant sweetpotato cultivar KO-12 (Daeyumi) is a promising biomaterial for the remediation of Pb-contaminated areas. The key genes involved in Pb tolerance in sweetpotato can be found by the comparative transcriptome analysis of the Pb-tolerant and -sensitive cultivars identified in this study. Further studies are needed for the field application of Pb-tolerant sweetpotato cultivars to Pb-contaminated soils and for the characterization of the tolerance of sweetpotato cultivars to other HMs.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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