BMC Plant Biology

RESEARCH

Open Access

Low concentrations of methyl jasmonate promote plant growth and mitigate Cd toxicity in *Cosmos bipinnatus*

Xiaofang Yu[1*†], Yujia Liu[1†], Liu Yang[1†], Yujing Liu[1], Chunyu Fan[1], Zihan Yang[1], Yuhan Xu[1], Xiaoxuan Zeng[1], Xue Xiao[2], Lijuan Yang[1], Ting Lei[1], Mingyan Jiang[1], Xi Li[1], Suping Gao[1] and Qi Tao[3]

Abstract

Cadmium (Cd) is a biologically non-essential heavy metal, a major soil pollutant, and extremely harmful to plants. The phytohormone methyl jasmonate (MeJA) plays an important role in plant heavy-metal resistance. However, the understanding of the effects of MeJA supply level on alleviating Cd toxicity in plants is limited. Here, we investigated how MeJA regulated the development of physiological processes and cell wall modification in *Cosmos bipinnatus*. We found that low concentrations of MeJA increased the dry weight of seedlings under 120 μM Cd stress by reducing the transport of Cd from roots to shoots. Moreover, a threshold concentration of exogenous MeJA increased the activities of superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) in plant roots, the concentration of Cd in the root cell wall, and the contents of pectin and hemicellulose 1 polysaccharides, through converting Cd into pectin-bound forms. These results suggested that MeJA mitigated Cd toxicity by modulating root cell wall polysaccharide and functional group composition, especially through pectin polysaccharides binding to Cd, with effects on Cd transport capacity, specific chemical forms of Cd, and homeostatic antioxidant systems in *C. bipinnatus*.

Keywords Cadmium, Methyl jasmonate, Cell wall, *Cosmos bipinnatus*

Introduction

Cadmium (Cd) is considered one of the most toxic non-essential elements in plants [1]; it not only hinders plant growth, but also affects human health through the food chain [2, 3]. It is currently listed among the top 10 most dangerous substances by the US Agency for Toxic Substances and Disease Registry [4]. Previous studies have sufficiently demonstrated that some exogenous materials can alleviate Cd toxicity, e.g., salicylic acid [5] and nitric oxide [6], which play important roles in growth, development, and defense. However, few studies have been conducted to explain the specific mechanisms by which exogenous substances mitigate Cd toxicity in plants.

Root systems are an important channel through which plants absorb heavy metal ions [7]. The cell wall (CW) is

†Xiaofang Yu, Yujia Liu and Liu Yang these authors contributed equally to this work.

*Correspondence:
Xiaofang Yu
xiaofangyu@sicau.edu.cn
[1]College of Landscape Architecture, Sichuan Agricultural University, Chengdu 611130, China
[2]Triticeae Research Institute of Sichuan Agricultural University, Chengdu, Sichuan 611130, China
[3]College of Resources, Sichuan Agricultural University, Chengdu 611130, China

the outermost structure of plant cells and therefore the first point of contact of plants with their environments. It has important chemical characteristics that make it highly adsorbent of heavy metals [8]. For most plants, the compartmentalization mechanism of the CW is one of the important mechanisms for detoxification and heavy metal tolerance. A large number of studies have shown that the CW is the major metal sink in plant roots. For example, Vázquez et al. [9] found that Cd deposited on the root cell wall (RCW) accounted for approximately 26–42% of total Cd in White lupin. Similarly, other studies reported that most of the Cd taken up by *Solanum nigrum* and *Athyrium wardii* was also stored in the RCW [8, 10]. The apoplast is mainly composed of the CW [11]. When metal ions enter plant roots through the apoplast pathway, they are affected by the polysaccharide components and functional groups of the RCW [12]. It is worth noting that the mechanism of CW coping with heavy metals is mainly based on polysaccharides as important binding sites for heavy metals, and its main components such as pectin (P), hemicellulose 1 (HC1), hemicellulose 2 (HC2) and cellulose content significantly affect the ability of CW to fix heavy metals; therefore, the variation of polysaccharides in plant RCW determines the amount of Cd fixation in RCW [13]. Yu et al. [14] reported that in *Oryza sativa* under Cd stress, the total Cd contents in P and HC1 of RCW were 71–85%; additionally, as the Cd concentration increased, the proportion of Cd in RCW P of the two rice lines increased significantly, while the proportion of Cd in HC1 decreased slightly. In *Ricinus communis*, Ren et al. [15] showed that under copper stress, 44.9–67.8% of the copper ions were accumulated in HC1, and only 11–25.9% and 14.1–26.6% of the copper ions were accumulated in HC2 and P, respectively. All of these previous results indicated that differences in the composition of CWs are the key factors mediating the tolerance of plant RCWs to heavy metals.

Jasmonic acid (JA) and methyl jasmonate (MeJA) are two key jasmonates, a family of cyclopentanone compounds synthesized from linolenic acid via the octadecanoic pathway [16]. Jasmonates are important factors in plant signal transduction and are involved in various abiotic stress responses [17, 18], such as in responses to drought stress [19], salt stress [20, 21], and cold stress [22, 23]. Recently, several studies have suggested that jasmonates may be involved in the regulatory processes associated with alleviating heavy metal stress. Application of exogenous JA or MeJA was able to increase the concentration of endogenous JA in *Solanum nigrum* under Cd stress and in *Avicennia marina* under combined Cd and copper (Cu) stress [24, 25], reflecting the important relationship between stress resistance and jasmonates. In the search for exogenous compounds that mitigate plant damage, researchers generally prefer MeJA to JA among jasmonates, as the initial rate of MeJA uptake by plants is faster than that of JA uptake; furthermore, MeJA is both inexpensive and safe [26]. In addition, exogenous MeJA reduced reactive oxygen species (ROS) synthesis in leaves and enhanced the activity of antioxidant enzymes and the concentration of ascorbic acid (AsA) in *Brassica napus* under arsenic (Ar) stress as well as *Kandelia obovata* under Cd stress [27, 28]. Moreover, many studies have indicated that MeJA has affected the degradation of CW by reducing cold damage in peach fruits, postharvest blueberries, and loquats [10, 29]. However, whether there is a direct link between MeJA and the CW and which of its components are involved in heavy metal accumulation remain unclear.

Cosmos bipinnatus Cav. (Asteraceae) has been widely cultivated owing to its high ornamental value, strong adaptability, and plasticity in adverse environments. Furthermore, *C. bipinnatus* is a potential Cr/Cd hyperaccumulator and Zn accumulator [30–32]. The CW was demonstrated to be the main site of Cd accumulation in roots of *C. bipinnatus* exposed to Cd. Under Cd stress, the gene encoding xyloglucan endotransglucosylase/hydrolase XTH was up-regulated, while glycosylphosphatidylinositol (GPI) and pectin methyl esterase (PME) in the sugar metabolism pathway were significantly up-regulated, which induced hemicellulose synthesis and P biosynthesis, thereby increasing the capacity of the CW to accommodate Cd and enhancing the Cd tolerance of *C. bipinnatus* [31]. According to our previous research, low concentrations of MeJA can alleviate the toxicity of Cd to *C. bipinnatus* seedlings, so we hypothesized that MeJA might alter the CW of *C. bipinnatus*, thereby enhancing the Cd resistance of the root system and alleviating the toxicity of Cd to the root system. The present study provides novel insights into the initial detoxification mechanism of exogenous MeJA at different concentrations in mitigating the toxicity of heavy metals in *C. bipinnatus* in order to determine the optimal concentration of MeJA to improve the Cd tolerance of *C. bipinnatus* seedlings. This study may provide new ideas for conservation applications of plants grown under unfavorable environmental stresses as well as Cd phytoremediation strategies.

The central aims of the present study were as follows: (1) to identify how MeJA regulates Cd absorption in *C. bipinnatus* and the subcellular distribution of Cd in its roots; (2) to study the effect of MeJA on ROS in roots under Cd stress; (3) to investigate the effects of MeJA on RCW structures and components with and without Cd. Accordingly, we also clarified the physiological mechanisms of MeJA that regulate the structure and components of RCWs to alleviate Cd toxicity in *C. bipinnatus*.

Materials and methods

Experimental material and plant culture conditions

Cosmos bipinnatus seeds, purchased from Huafeng Seed Company (Jiangsu, China), were surface sterilized with 2% NaClO for 20 min and germinated in clean perlite at 25 °C for 7 days. Uniformly growing seedlings were transplanted into plastic pots (21 cm × 28 cm × 11 cm, 60 plants per pot) containing 5 L of half-strength Hoagland solution (1 mM $NH_4H_2PO_4$, 6 mM KNO_3, 4 mM Ca $(NO_3)_2{\cdot}4H_2O$, 2 mM $MgSO_4{\cdot}7H_2O$, 10 μM H_3BO_3, 1.8 μM $MnSO_4$, 0.3 μM $CuSO_4$, 5 μM $ZnSO_4$ and 50 μM Fe (III)-EDTA, pH 6.5), which was replaced with full-strength Hoagland nutrient solution after 14 days. Then, the 18 plastic pots were randomly divided into the following six treatments, with Cd and MeJA solutions added to the Hoagland solution according to the following treatments, each with three replicates: 0 μM $CdCl_2$+0 μM MeJA (CK), 120 μM $CdCl_2$+0 μM MeJA (Cd treatment alone), 120 μM $CdCl_2$+0.1 μM MeJA (Cd+MeJA1), 120 μM $CdCl_2$+1 μM MeJA (Cd+MeJA2), 120 μM $CdCl_2$+10 μM MeJA (Cd+MeJA3), 120 μM $CdCl_2$+100 μM MeJA (Cd+MeJA4). Plants were grown in a growth chamber at 25 °C, 70% relative humidity, and 500 μM m^{-2} photon flux density. After 7 days of treatment, seedlings were harvested. Shoot and root samples were collected from each treatment and rapidly frozen in liquid nitrogen to determine the subcellular distributions of Cd, and the other samples were assayed for their dry weight and Cd concentrations.

Phenotype characterization and metal concentrations

The harvested samples were divided into their aboveground and belowground parts, cleaned of surface Cd ions, and divided into two subsamples for subsequent testing. One of the subsamples was dried in an oven at 105 °C for 30 min and then dried further at 70 °C until a constant weight was reached, and the dry weight was measured as an indicator of biomass (10 plants per biological replicate, with three replicates). Afterwards, 0.2 g of each dry sample was digested with an acid solution [HNO_3/$HClO_4$ (4/1, *v*/*v*)] at 180 °C for 8 h. The suspensions were diluted to 50 mL with deionized water and filtered through filter paper. The concentrations of Cd in the final solutions were detected by ICP-MS (7900, Agilent Technologies, Santa Clara, CA, USA). The reference standard solution was purchased from Guobiao Testing and Certification Company (Beijing, China). The translocation factor (TF) was calculated as described by Dai et al. [33].

The Cd subcellular distribution was determined according to the method of Su et al. [34] with some modifications. Fresh samples (1 g) were homogenized with 50 mM Tris-HCl buffer solution (pH 7.5) containing 250 mM sucrose, 1.0 mM DTE ($C_4H_{10}O_2S_2$), and 5.0 mM ascorbic acid. Then, the mixture was centrifuged at 1000 × *g* for 15 min at 4℃, and the obtained precipitate was designated as the CW fraction. The supernatant solution was further centrifuged at 15,000 × *g* for 30 min. The resultant pellet and supernatant solution were designated as the organelle-containing fraction and soluble fraction, respectively. All fractions were dried and then were digested in 5 mL of HNO_3. The Cd concentrations in the different fractions were analyzed by flame atomic absorbance spectrometry (FAAS; Shimadzu AA-6300; Shimadzu, Kyoto, Japan). The limit of Cd detection was 0.02 mg L^{-1}.

Chemical forms of cd in *Cosmos bipinnatus* roots

Six chemical forms of Cd were extracted successively, as described by Wang et al. [35] and Wang et al. [36]. Then, frozen sample material (1 g) that had been cut into small pieces was mixed with 10 mL of the extracts mentioned above and soaked at 25℃ for 22 h. Each extract was collected, and the residual material was re-extracted with 10 mL of extraction solution twice. Three replicate extraction solutions of each of the chemical forms were merged together and digested in an acid solution [HNO_3:$HClO_4$ (4:1, *v*/*v*)]. The concentrations of Cd in their different chemical forms were assayed by FAAS using the Shimadzu AA-6300 instrument.

Determination of three antioxidant enzymes in roots and shoots

Approximately 0.5-g samples of fresh leaf or root tissue were homogenized in 5 mL of 50 mM Tris-HCl buffer (pH 7.0) containing 1 mM EDTA, 1 mM DTT, 5 mM $MgCl_2$, 1 mM AsA, and 1 mM glutathione (GSH) [37]. The homogenate was then centrifuged at 9000 × *g* for 20 min at 4℃, and the extract was used for enzyme assays.

Furthermore, following the method described by Knörzer et al. [37], the superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) enzymes were extracted, and then, their activity levels were determined by nitroblue tetrazolium (NBT) photoreduction [38], the guaiacol method [39], and a method previously described by de Azevedo Neto et al. [40], respectively.

Determination of cd in root symplast and apoplast sap

The Cd content of the sap from root symplast and apoplast was determined using the method of Redjala et al. [41]. (1) Apoplast sap was extracted as follows. First, 2.0–5.0 g of fresh root tissue was weighed, cut to lengths of 0.2–0.5 cm, and extracted with 50 mL of deionized water for 24 h. The extract was filtered, and the filtrate was collected for testing. (2) Symplast sap was extracted as follows. Again, 2.0–5.0 g of fresh roots were weighed, cut to lengths of 2.0–5.0 cm, and extracted with 50 mL

of deionized water for 24 h. The extract was filtered out, leaving the residue behind, which was added to a mortar, ground with quart sand, dissolved with a small amount of deionized water after the plant tissue was homogenized, diluted to 50 mL, shaken for 1, and finally filtered to obtain the filtrate for testing. The concentration of Cd in the filtrate was measured by the flame atomic absorption method using a Shimadzu AA-6300 instrument.

Determination of RWC polysaccharides

Extraction and determination of RCW fractions

The RCW was extracted according to the method described by Zhu et al. [42]. Liquid nitrogen was added to fresh root samples (1 g), which were ground into powder in a mortar, dissolved with 5 mL of 75% ethanol, and transferred to a 10-mL centrifuge tube. After incubation on ice for 30 min, samples were centrifuged at 8000 × *g* for 10 min, and the supernatant was discarded. Then, to each sample was added 5 mL of ice-cold acetone and methanol: chloroform (1:1) for methanol extraction (each time adding organic reagents, followed by an ice bath for 20 min, centrifugation at 8000 × *g*, and discarding of the supernatant). The above steps were repeated, each time collecting the precipitate, which was obtained after being washed with methanol, leaving behind the extracted RCW, which was dried with a vacuum freeze dryer and stored at 4 °C.

Separation of RCW polysaccharides

According to the method of Yang et al. [43], the primary CW extract was further separated into P, HC1, and HC2 fractions. The freeze-dried CW was weighed into 10-mg subsamples and put into a 10-mL centrifuge tube, to which was added 5 mL of double distilled water. Subsamples were then placed in boiling water for 1 h and then centrifuged at 13,000 × *g* for 20 min. The supernatant was transferred to another 10-mL centrifuge tube, to which was added 3 mL of double-distilled water, and after this was repeated three times, the P fraction extraction was considered complete. Then, each sample received an addition of 5 mL of 0.1% $NaBH_4$, and the 4% KOH alkaline solution was extracted overnight, followed by centrifugation at 13,000 × *g* for 20 min. The supernatant was transferred to another 10-mL centrifuge tube, and the process was repeated once. The combined supernatant contained the HC1 fraction; finally, residues received an addition of 5 mL of 0.1% $NaBH_4$ and 24% KOH alkaline solution for overnight extraction, followed by centrifugation at 13,000 × *g* for 20 min. The resulting supernatant was placed in a 10-mL centrifuge tube, and after the process was repeated once, the two supernatants were combined to obtain the HC2 fraction (Fig. 1).

Determination of RCW polysaccharide content

The determination of RCW polysaccharide content utilized the method described by Li et al. [44]. Volumes of glucose standard solution (0.01 g/100 mL) of 0, 0.2, 0.4, 0.6, 0.8, 1.0, 1.6, and 2.0 mL were each added to their own test tube with a stopper, diluted to a volume of 2 mL, and then placed in an ice bath. First, a micropipette was used to add 0.1 mL of 80% phenol to each of the samples, which were then shaken and mixed. Then, 10 mL of concentrated sulfuric acid solution was added to each of the samples, which were then mixed and allowed to sit for 15 min. Samples were then boiled in a water bath for 15 min, cooled to room temperature, and measured for absorbance at a 490 nm wavelength, with 2 mL of deionized water used as the blank.

Determination of total sugar content in the sample utilized deionized water as a blank solution and followed the same method as described above. Then, 0.4 mL of the P extract sample, 0.74 mL of the HC1 exact sample, and 0.6 mL of the HC2 extract sample were each diluted to 2 mL with deionized water, and the sugar content of each sample was determined. Using a standard curve, the absorbance value was measured to calculate the total sugar content of the polysaccharide component of the P fraction in the CW of the *C. bipinnatus* root samples grown under the same Cd treatment with different exogenous MeJA concentrations, as well as corresponding HC1 and HC2 total sugar content values.

Determination of cd content in polysaccharides of *C. bipinnatus* RCW

A 3-mL volume of the RCW components (P, HC1, HC2) was added to a digestion tube, along with an acid solution [HNO_3:$HClO_4$ (4:1, *v*/*v*)]. Digestion was performed at 320 °C. The Cd content was determined by the flame atomic absorption spectroscopy method using a Shimadzu AA-6300 instrument.

Fourier transform infrared spectroscopy analysis of RCW

The RCW of *C. bipinnatus* treated with different concentrations of MeJA and the RCW of CK plants were characterized by Fourier transform infrared spectroscopy (FTIR). Subsamples of the freeze-dried samples (1 mg) were weighed and then mixed with crushed crystalline potassium bromide (1:100, *w*/*w*). Then the samples were grinded thoroughly in an agate mortar and pressed into a tablet for FTIR determination. FTIR (Nicolet 670; Thermo Scientific, Waltham, MA, USA) was used to record the spectral signal information in the range of 4000–400 cm^{-1}, with a spectral resolution of 4 cm^{-1}.

Statistical analysis

The test data were analyzed using Excel 2010 (Microsoft Corp., Redmond, WA, USA) and SPSS 24 (IBM

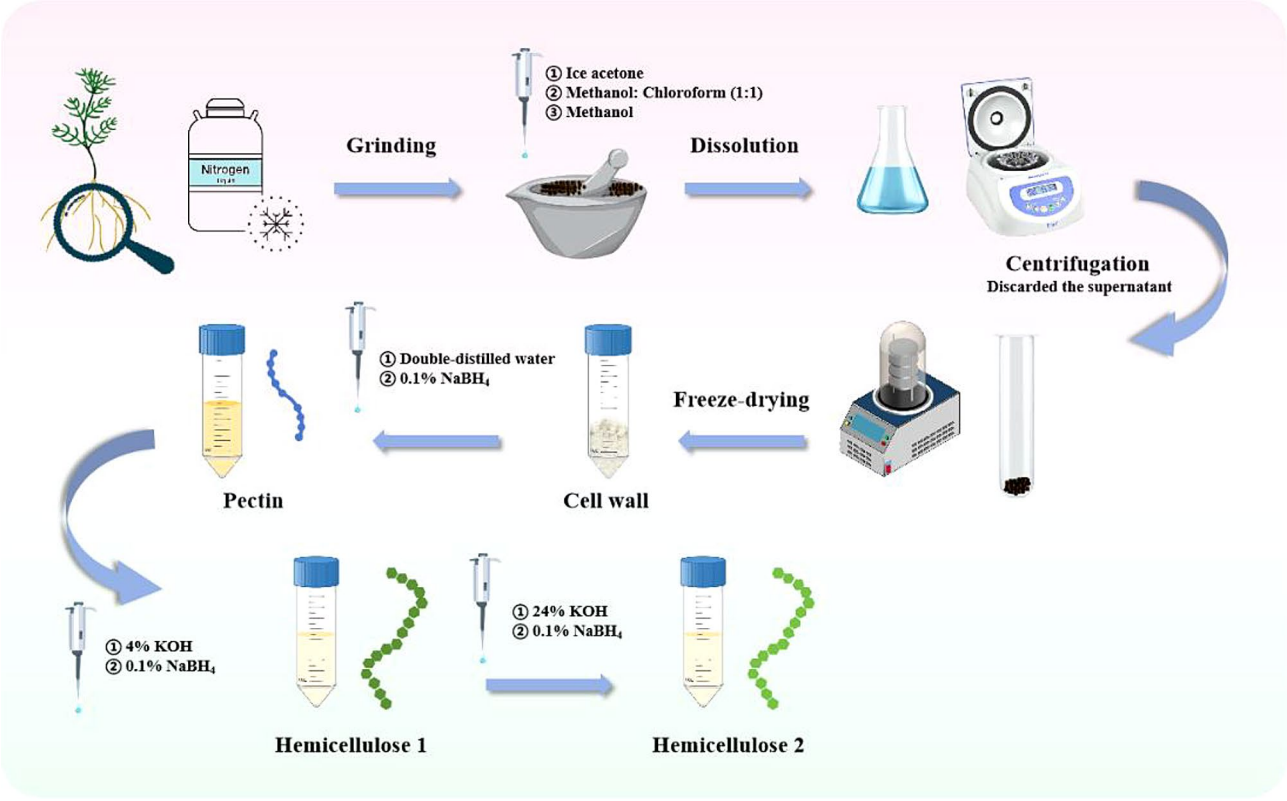

Fig. 1 Flow chart for extraction of *Cosmos bipinnatus* cell wall and cell wall components

Corp., Armonk, NY, USA) software. One-way analysis of variance and Duncan's multiple range test were used to determine significant differences in Cd content and related variables between samples from plants grown under different MeJA concentration treatments under the same Cd stress at a significance level of $p < 0.05$.

Results

Effect of exogenous MeJA on cd uptake of *C. bipinnatus*

In our preliminary experiment, 120 μM Cd treatment damaged *C. bipinnatus* plants. Therefore, the effect of MeJA was explored under this Cd concentration treatment. Seven days after the application of 120 μM Cd, the root and shoot dry weights of *C. bipinnatus* had decreased significantly. The addition of exogenous MeJA (0.1 μM, 1 μM, and 10 μM) increased the biomass of *C. bipinnatus* seedlings under Cd stress. In particular, 1 μM MeJA treatment significantly increased the aboveground and belowground dry mass of *C. bipinnatus*. However, high concentrations of MeJA (100 μM) did not significantly affect *C. bipinnatus* biomass compared to Cd treatment alone (Fig. S1). The Cd content of *C. bipinnatus* under the various treatments is shown in Fig. 2-A, B; while MeJA concentrations of 100 μM and especially 1 μM reduced the Cd content in the roots, under MeJA concentrations of 0.1 and 10 μM, the Cd content in roots increased obviously. In addition, low concentrations of exogenous MeJA (0.1, 1 μM) did not change the Cd content in the shoots of *C. bipinnatus* obviously, but higher concentrations of exogenous MeJA (10, 100 μM) reduced the Cd content in the shoots. After analyzing the translocation factors, we found that 1 μM MeJA significantly facilitated the transport of Cd, and the TFs increased by 6.06% compared with Cd treatment alone, respectively (Fig. 2-C).

Effects of MeJA on subcellular distribution of cd in *C. bipinnatus*

To determine whether various concentrations of MeJA affected Cd detoxification or Cd toxicity, we assayed the Cd subcellular distribution in root and shoot tissues. Compared with Cd treatment alone, application of 0.1 and 1 μM MeJA significantly reduced the Cd concentration in the CW fraction under 120 μM Cd stress (Fig. 3-A), while the other two fractions, i.e., the organelle-containing and soluble fractions, showed no significant differences among treatments. Thus, lower concentrations of MeJA reduced the total Cd concentration in the aerial tissues. The Cd subcellular distribution patterns in roots differed from those in shoots. Various MeJA treatments significantly increased the Cd concentrations in the CW fraction compared with Cd treatment

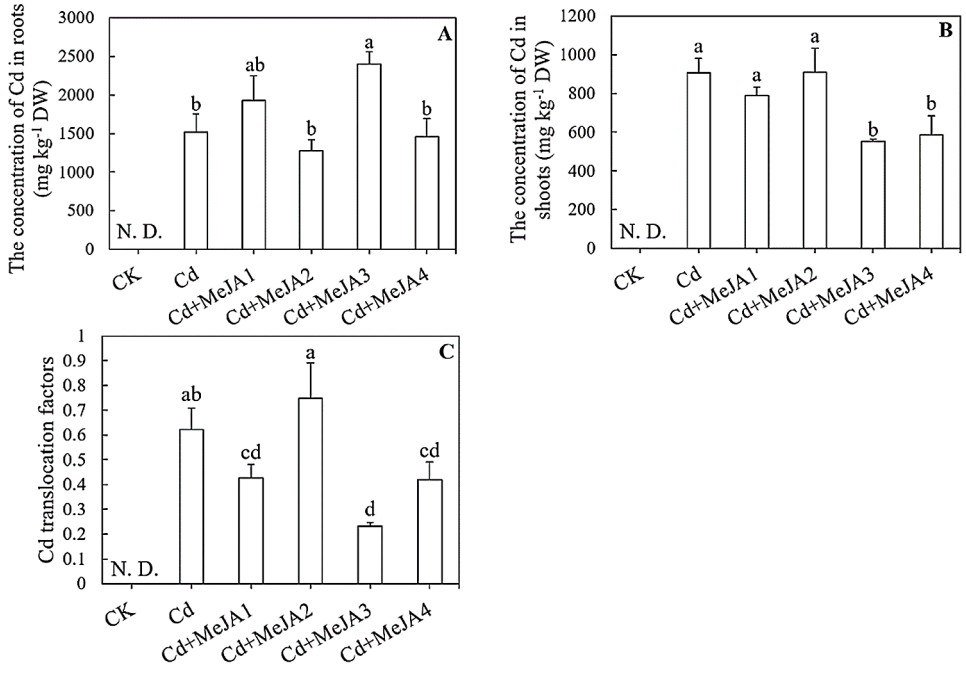

Fig. 2 Effect of different concentrations of methyl jasmonate (MeJA) on Cd concentration and their translocation factors (TFs) in *Cosmos bipinnatus*. **A**, Cd concentrations in roots. **B**, Cd concentrations in shoots. **C**, Cd translocation factors. The values shown are the means ± standard error ($n = 3$). Bars labelled with different letters were significantly different among treatments at $p < 0.05$. N.D., not detected; Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

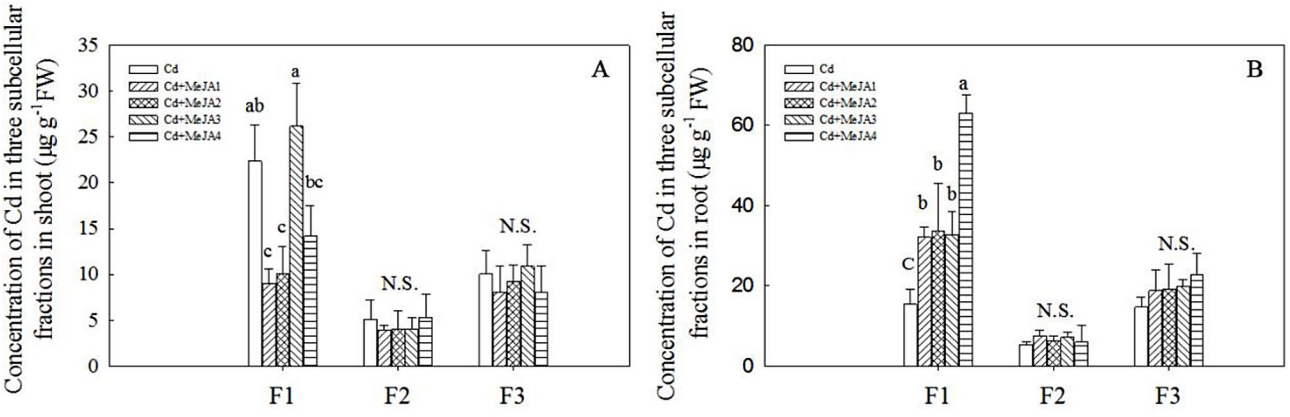

Fig. 3 Effect of different concentrations of methyl jasmonate (MeJA) on the subcellular distribution of Cd. **A**, Concentration of Cd in three subcellular fractions of shoot tissue. **B**, Concentration of Cd in three subcellular fractions in root tissue. The values shown are means ± standard deviations of three biological replicates. Values followed by different lowercase letters differed significantly at $p < 0.05$. N.S., not significant; F1, cell wall fraction; F2, organelle-containing; F3, soluble fraction; Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

alone, while the organelle-containing and soluble fractions showed no significant difference among treatments (Fig. 3-B). The results not only suggested that binding of Cd in the RCW fraction may be related to Cd detoxification induced by the various MeJA treatments, but also indirectly indicated that various MeJA concentrations increased total Cd concentrations in roots. The chemical forms of Cd in root tissue were assayed to determine whether application of MeJA positively affected Cd detoxification.

Effects of MeJA on chemical forms of cd accumulated in *C. bipinnatus* roots

The measurement of different chemical forms of Cd in plant roots at day 7 is shown in Fig. 4. NaCl-extractable Cd was the largest proportion in the roots of plants grown under various treatments, followed by ethanol-,

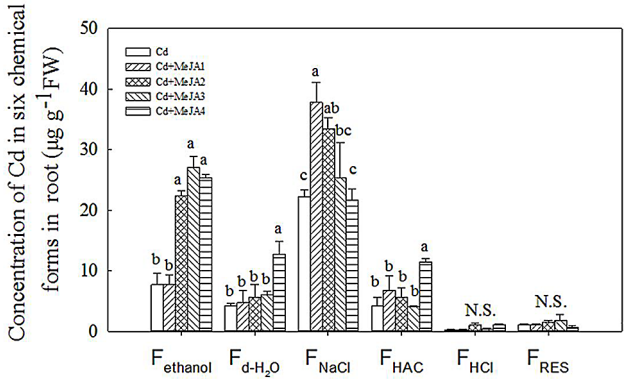

Fig. 4 Effect of different concentrations of methyl jasmonate (MeJA) on chemical forms of Cd. The values presented are means ± standard deviations of three biological replicates. Values followed by different lowercase letters are significantly different at a threshold of $p < 0.05$. N.S., not significant; $F_{ethanol}$, extraction of inorganic Cd, including nitrate/nitrite, chloride, and aminophenol Cd; Fd-H_2O, extraction of water-soluble Cd in the form of organic acid complexes and Cd $(H_2PO_4)_2$; F_{NaCl}, extraction of P-integrated Cd; F_{HAC}, extraction of insoluble $CdHPO_4$ in the form of organic acids and Cd $(H_2PO_4)_2$ and other Cd-phosphate complexes; F_{HCl}, extraction of oxalate acid-bound Cd; F_{RES}, Cd in residues; Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

d-H_2O- and acetic acid (HAC)-extractable forms, while other chemical forms of Cd were rather low (Fig. 4). Additionally, 1–100 μM MeJA treatments under 120 μM Cd significantly increased the Cd concentration in ethanol extract, while 0.1–1 μM MeJA treatments significantly enhanced the NaCl-extractable Cd. Only 100 μM MeJA significantly raised the Cd concentration in d-H_2O and HAC extracts.

Malondialdehyde concentration and activities of antioxidant enzymes in roots

Under Cd stress, malondialdehyde (MDA) content of plant roots increased significantly. Compared with Cd treatment alone, MDA content increased with MeJA concentration, and the MDA content under the 0.01 μM concentration treatment did not significantly differ from that of the control (Fig. 5-A).

The trends in SOD and POD activities were similar, and both significantly increased under Cd stress alone and decreased under low concentrations of exogenous MeJA. Compared with CK plants, the activity levels of SOD and POD increased by 35% and 38%, respectively (Fig. 5-B). Additionally, their activities were all increased under treatments with other concentrations of MeJA. CAT activity decreased under Cd treatment alone, but it increased after the application of exogenous MeJA, especially under low-concentration MeJA treatment, in which CAT activity was 1.75 times higher than that under Cd treatment alone (Fig. 5-C, D).

The effect of exogenous MeJA on cd absorption

Cd concentration in the root apoplast pathway accounts for 82.7%, 82.7%, 83.3%, 80.9%, and 78.9% of Cd content under Cd, Cd + MeJA1, Cd + MeJA2, Cd + MeJA3, and Cd + MeJA4 treatments, respectively, about 4 times more than the Cd content of the symplast pathway (Table 1). Additionally, the Cd content in the root symplast and apoplast samples decreased when treated with the relatively lower concentrations of MeJA (0.1, 1, 10 μM), but increased when treated with the highest tested concentration of MeJA (100 μM). Thus, appropriate concentrations of exogenous MeJA (0.1, 1, 10 μM) were able to inhibit the absorption of Cd by roots and played a somewhat protective effect on the physiological functions of the roots.

Exogenous MeJA affects the polysaccharide content of *C. bipinnatus* RCW

Compared with Cd stress, there were no significant changes in RCW P content under of the lower applied concentrations of MeJA (0.1, 1, 10 μM); in contrast, under high concentrations of MeJA (100 μM), the P content was apparently increased (Fig. 6-A). Under treatment with different concentrations of MeJA (0.1, 1, 10, 100 μM), the content of HC1 was significantly increased (Fig. 6-B). However, the trend in HC2 content was opposite of that of HC1. HC2 content did not obviously change under 1 and 100 μM MeJA treatments, while under the 0.1 and 10 μM MeJA treatments, the content of HC2 was obviously lower than that under Cd treatment alone (Fig. 6-A, C).

Effects of exogenous MeJA on the binding of cd to polysaccharides in the RCW

Compared with Cd treatment alone, as MeJA concentration increased, the content of Cd in the P and HC1 fractions increased first and then decreased. Low concentrations of MeJA (0.1, 1 μM) did not obviously change the amount of Cd bound in the P fraction, while high concentrations of MeJA (10, 100 μM) significantly increased amount of Cd bound. In addition, under all tested concentrations of MeJA (0.1, 1, 10, 100 μM), the amount of Cd bound in HC1 increased, and it reached its highest value under the 1 μM MeJA treatment. In contrast, the amount of Cd bound in HC2 increased obviously, except under the 1 μM MeJA treatment (Fig. 7-A, C). Further analysis of the CW polysaccharide components of the P, HC1, and HC2 fractions under Cd treatment alone revealed the binding ability of Cd, as shown in Fig. 7-D. In the polysaccharide component of the *C. bipinnatus* RCW, the main component that bound Cd was P. The Cd binding capacity of P accounted for 97.05% of bound Cd, while HC1 and HC2 only accounted for 2.85% and 0.33%, respectively.

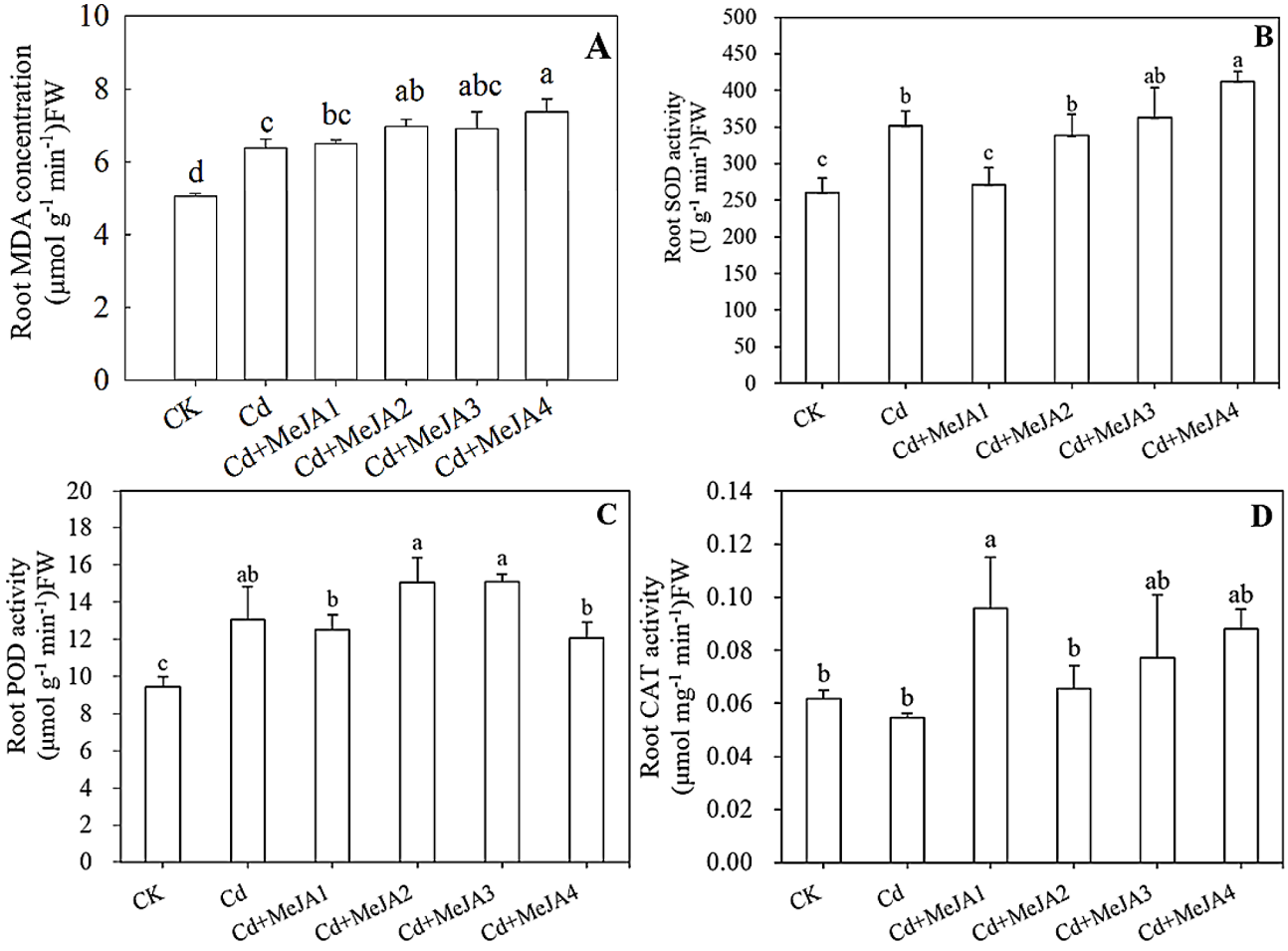

Fig. 5 Effect of different concentrations of methyl jasmonate (MeJA) on malondialdehyde (MDA) concentration, superoxide dismutase (SOD) activity, peroxidase (POD) activity, and catalase (CAT) activity in roots of *Cosmos bipinnatus*. **A**, MDA concentration. **B**, SOD activity of roots. **C**, POD activity of roots. **D**, CAT activity of roots. The values shown are means ± standard deviations of three biological replicates. Values followed by different lowercase letters are significantly different at a threshold of $p < 0.05$. Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

Table 1 Cd concentrations in root symplast and apoplast samples of *Cosmos bipinnatus* under different treatments

Transportation pathway	Cd	Cd + MeJA1	Cd + MeJA2	Cd + MeJA3	Cd + MeJA4
Symplast (mg kg^{-1})	10.70 ± 0.13b	7.10 ± 0.47d	9.34 ± 0.82c	8.69 ± 0.29c	14.69 ± 0.14a
Apoplast (mg kg^{-1})	51.05 ± 1.02b	33.87 ± 1.54d	46.65 ± 2.08c	36.70 ± 2.26d	54.96 ± 3.10a

Note Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA; MeJA, methyl jasmonate. The values shown are the means ± standard error ($n = 3$). Values labeled with different letters indicate significant differences among the different treatments at $p < 0.05$

Correlation analysis

Pearson correlation analysis was performed on the polysaccharide content of the RCW, the concentration of MeJA, and the Cd content of each component.

As shown in Fig. 8-A, among the P components of the RCW, the content of P and the concentration of exogenous MeJA showed a very significant positive correlation ($p < 0.01$, $r = 0.9771$). However, the contents of both HC1 and HC2 in the RCW were not significantly correlated with the concentration of exogenous MeJA (Fig. 8-B, C).

CW functional groups influenced the accumulation of cd in *C. bipinnatus*

By analyzing the FTIR spectra of the *C. bipinnatus* RCW under different treatments, relevant information on its characteristic peaks can be obtained [45]. According to the FTIR diagram of *C. bipinnatus* CW treated with Cd alone and in combination with different concentrations of MeJA, the absorption peaks of wavenumbers 3400, 2920, 1640, 1240, and 1060 cm^{-1} all changed. Additionally, their peaks were also somewhat deflected (Fig. 9). By comparing the blank control group with the treatment

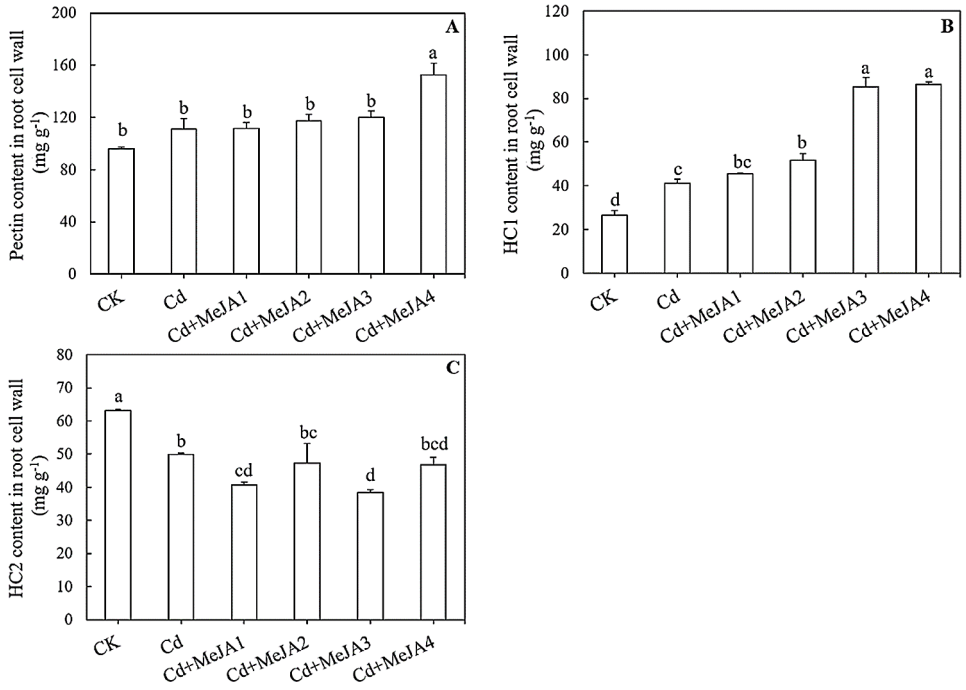

Fig. 6 Effects of methyl jasmonate (MeJA) treatment on the content of polysaccharides in the cell wall of *Cosmos bipinnatus* roots. **A**, The content of pectin (P). **B**, The content of hemicellulose 1 (HC1). **C**, The content of hemicellulose 2 (HC2). The values shown are means ± standard deviations of three biological replicates. Values followed by different lowercase letters are significantly different at a threshold of $p < 0.05$. Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

group subjected to Cd stress alone, we found that the absorption peak at 3400 cm^{-1} was significantly reduced, and several characteristic absorption peaks at other wavenumbers were also offset to some extent (Fig. 9). Under Cd stress, the FTIR diagram of plant RCW also differed when different concentrations of MeJA were added. In particular, the absorption peaks near 3400, 2920, and 1240 cm^{-1} were shifted to high frequencies, and the maximum shift near 3400 cm^{-1} amounted to 19.4, indicating that MeJA had a strong influence on the proteins, fatty acids, and various carbohydrates in the CW of *C. bipinnatus*, thus affecting the contents of -NH and -OH in the CW. Additionally, the maximum shift near 2920 cm^{-1} amounted to 6.3, indicating that MeJA affected the hydrophilic esters in the pectin of *C. bipinnatus* CW, thus affecting the content of $-CH_3$, while the maximum shift near 1240 cm^{-1} was 9.1, indicating that MeJA affected the contents of -C-O-S, -C-O, and/or -C-O-P in the CW of *C. bipinnatus*.

Discussion

Low concentrations of MeJA had protective effects on *C. bipinnatus*

In our previous study, we found that *C. bipinnatus* showed visible symptoms of toxicity under 120 μM Cd stress. Applying MeJA together with Cd enables investigation of the interaction between MeJA and Cd. We previously found that 1 μM MeJA alleviated the adverse effect of Cd stress on seed germination [31]. In the present study, an appropriate concentration of MeJA also relieved some damage associated with Cd toxicity, which is accordance with the findings of Kolupaev et al. [46], who found that when plants are under stress caused by low temperatures, heavy metals, and diseases, MeJA and other hormones rapidly accumulate in the plant body to increase the antioxidant level of cells and protect membranes and proteins; thus, MeJA can reduce the impact of adverse conditions on plant growth. Moreover, the addition of low concentrations of MeJA was observed to promote the transfer of Cd from the roots to the aboveground shoots (Fig. 2), which may enhance plant tolerance to heavy metals [28]. These results suggested that low concentrations of MeJA alleviated some negative effects of Cd in plants. Previously, the appropriate application of MeJA was also found to mitigate the toxicity of heavy metals to plants by reducing ROS synthesis, inducing the activity of antioxidant enzymes, and increasing the levels of AsA and GSH [47]. In addition, low concentrations of MeJA can promote plant growth and development by promoting plant root growth and regulating the expression of key genes in the synthesis and transport pathways of other internal hormones, such as JA, growth hormone and gibberellin, which can improve the Cd tolerance of plants [48, 49]. However, the mechanism by which MeJA alleviates stress has not been completely demonstrated yet. Exogenous plant hormones may affect

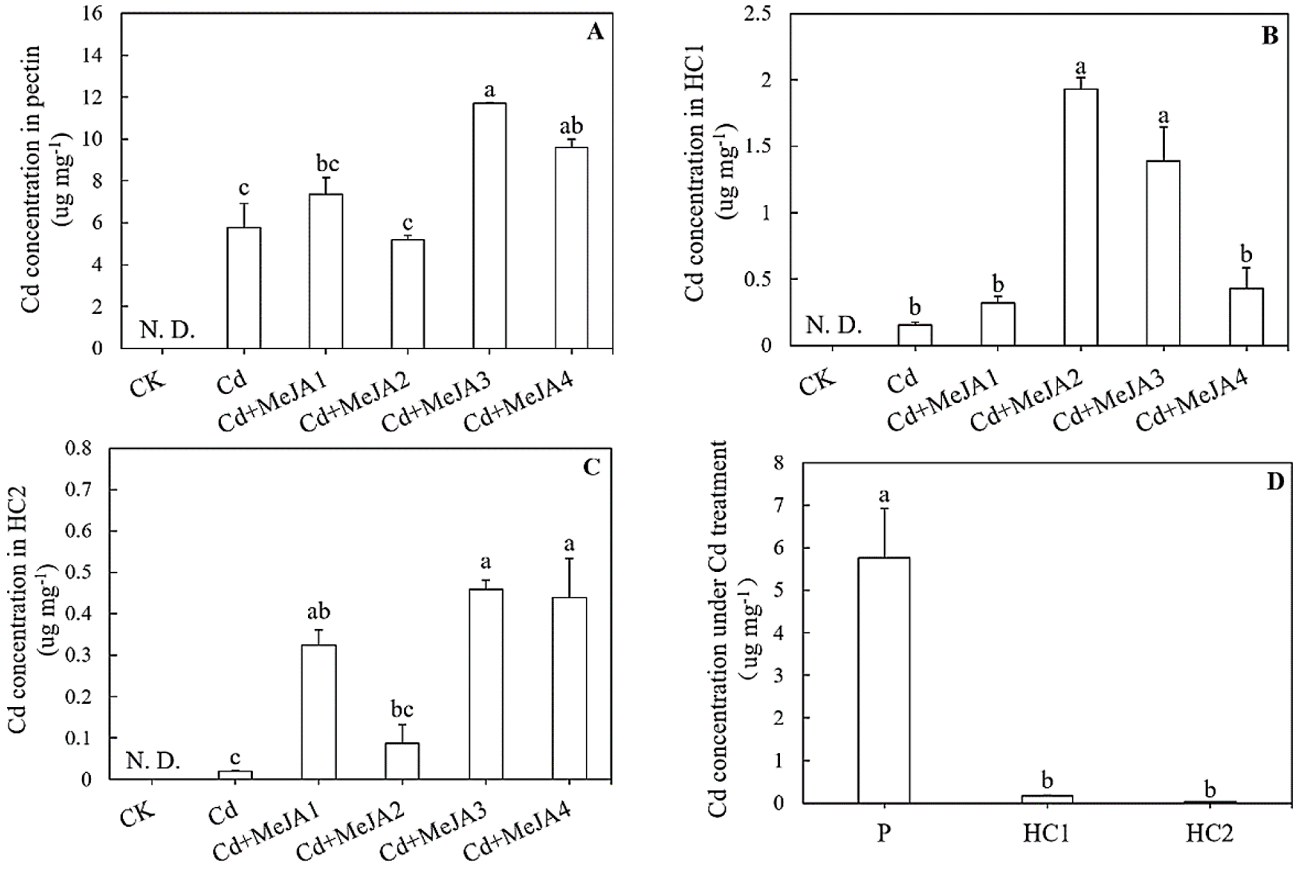

Fig. 7 Cd content in cell well polysaccharides treated with different methyl jasmonate (MeJA) treatments. **A**, Cd content in the pectin (P) fraction. **B**, Cd content in the hemicellulose 1 (HC1) fraction. **C**, Cd content in the hemicellulose 2 (HC2) fraction. **D**, Cd concentration in P, HC1, and HC2 fractions under Cd treatment alone. The values shown are means ± standard error ($n = 3$). Bars labelled with different lowercase letters indicate significant differences among treatments at a threshold of $p < 0.05$. N.D., not detected; Cd, 120 μM $CdCl_2$; Cd + MeJA1, 120 μM $CdCl_2$ + 0.1 μM MeJA; Cd + MeJA2, 120 μM $CdCl_2$ + 1 μM MeJA; Cd + MeJA3, 120 μM $CdCl_2$ + 10 μM MeJA; Cd + MeJA4, 120 μM $CdCl_2$ + 100 μM MeJA

the distribution and chemical forms of heavy metals to enable detoxification, e.g., the application of exogenous phytohormones to perennial ryegrass and *Brassica parachinensis* can lead to a reduction in the content of their heavy metal chemical forms and a shift to less toxic forms [50, 51]. Notably, our study found that MeJA had some influence on both the subcellular distribution and chemical forms of Cd (Fig. 10).

MeJA affected the subcellular distribution of cd

The root cell constituents analyzed in the present study are comprised of three categories: the CW fraction, the soluble fraction, and the organelle-containing fraction. The soluble fraction mainly includes the contents of the vacuole. Comprised of polysaccharides (including cellulose, HC, and P) and proteins, the CW is the first structure to contact outer substance [52]. The 0.1 and 1 μM MeJA treatments decreased the Cd concentration in the CW fraction and had no effect on the other two fractions, indicating that some Cd may be obstructed by CWs. Cd in roots is taken up into aerial tissues using some key heavy metal transporters [53]. MeJA may induce the expression of heavy metal transporters to promote Cd uptake. Under Cd stress, plants underwent changes in many aspects, including in their cell structure, photosynthesis, and stomatal shape and number [54]. Therefore, MeJA may affect the transpiration of *C. bipinnatus* by inducing stomatal regulation that ultimately enhances Cd transport. However, this requires further confirmation. Various MeJA treatments significantly increased the Cd concentration in RCWs compared with Cd treatment alone (Fig. 3-B), while the other two fractions showed no significant difference. Polysaccharides bind with metals to decrease their movement [55]. These results indicated that MeJA may induce polysaccharides to bind with Cd, thus enhancing the Cd tolerance of *C. bipinnatus* (Fig. 10). This has also been found in tomato studies, where the application of MeJA to tomato promoted the enrichment of Cd in RCW and mitigated the toxic effects of Cd on tomato seedlings [56].

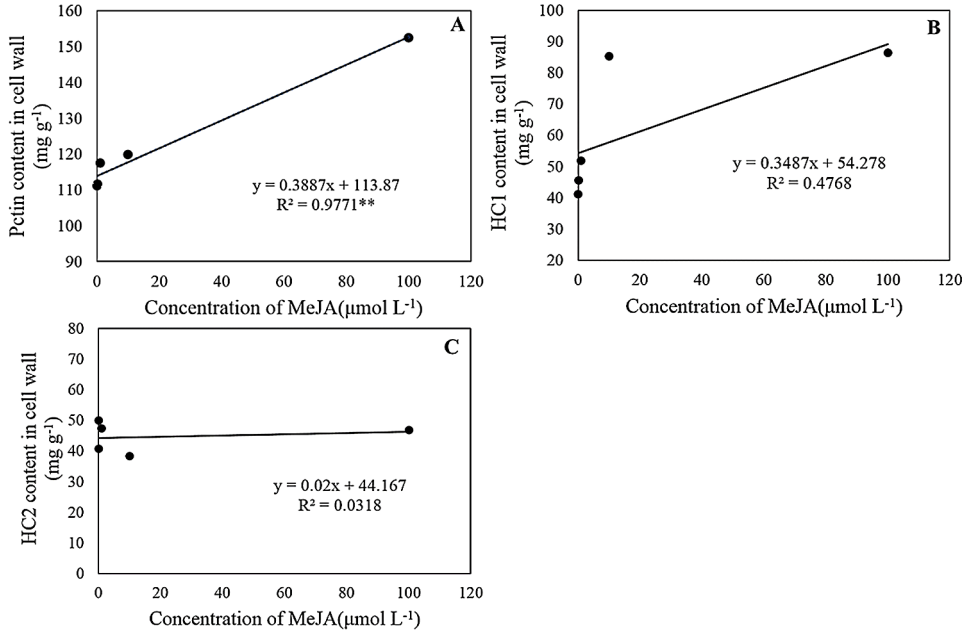

Fig. 8 Correlation between root cell wall (RCW) polysaccharide composition and concentration of methyl jasmonate (MeJA). **A**, Correlation between pectin (P) content and MeJA concentration. **B**, Correlation between hemicellulose 1 (HC1) content and MeJA concentration. **C**, Correlation between hemicellulose 2 (HC2) content and MeJA concentration

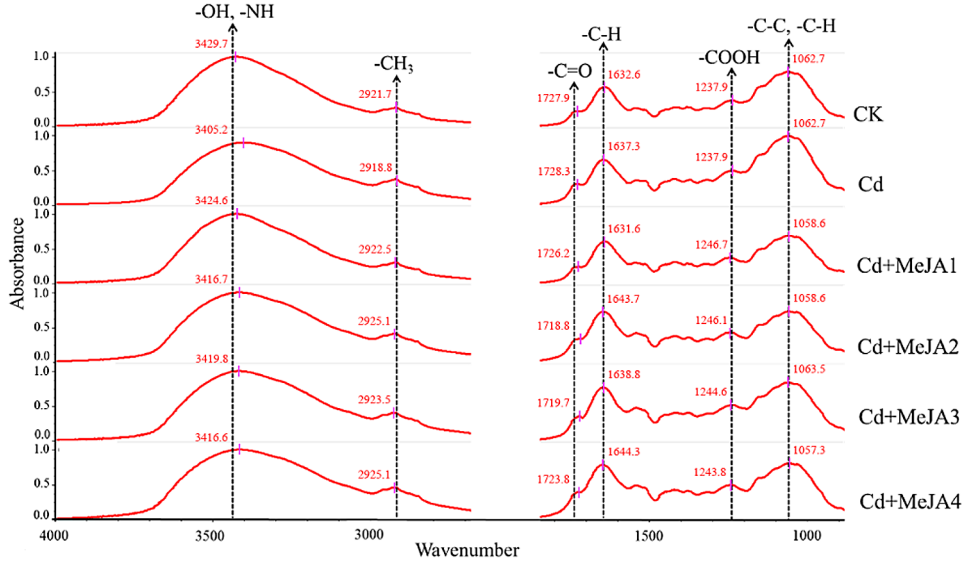

Fig. 9 Fourier transform infrared (FTIR) spectra of the root cell wall (RCW) of *Cosmos bipinnatus* under different treatments

MeJA affected cd chemical forms

Heavy metal chemical forms can be divided into two forms: mobile forms, including ethanol-extractable and d-H_2O-extractable forms, which are easy to be transported, and immobile forms, including NaCl-extractable and HAC-extractable forms. These immobile forms are closely related to the migration and toxicity of heavy metals in plants [34]. NaCl-extractable forms included P integrated with Cd, while HAC-extractable forms included phosphate-bound Cd. Our findings revealed that 0.1–1 μM MeJA treatments significantly enhanced the Cd concentration in NaCl-extractable Cd compared with Cd treatment alone, indicating that lower MeJA concentrations may stimulate more P to bind with Cd to limit Cd mobility (Fig. 4). P is one of the basic CW components, and it is a major contributor to Cd immobilization [57]. Therefore, 0.1–1 μM MeJA could enhance Cd uptake capacity of the CW and strengthen the Cd tolerance of *C. bipinnatus*. Similarly, application of phosphorus to Cd-stressed oilseed rape increased the proportion of Cd in

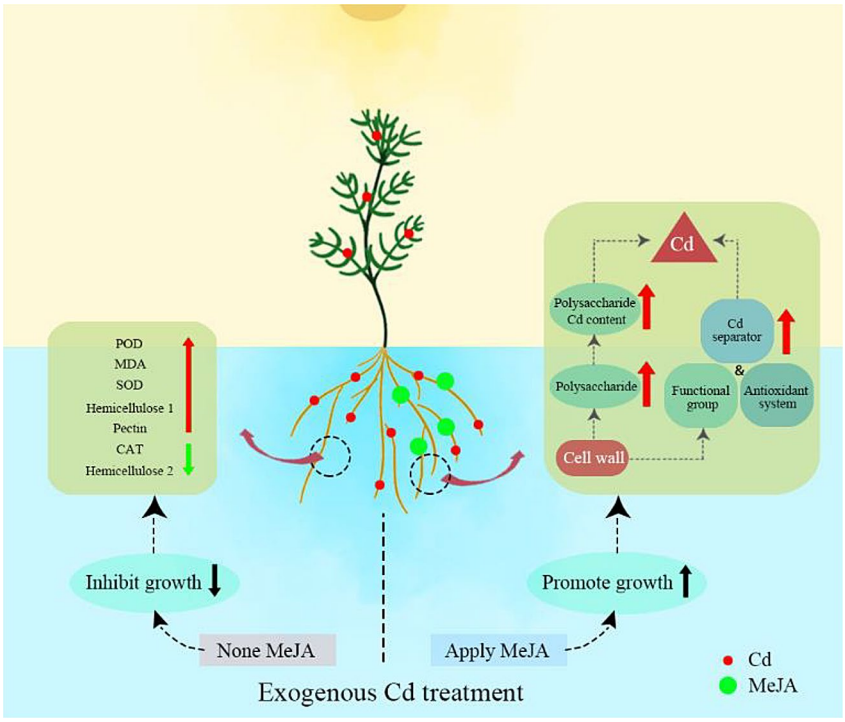

Fig. 10 Effect of different concentrations of methyl jasmonate (MeJA) on the Cd adsorption mechanism of *Cosmos bipinnatus*

the NaCl-extracted state of oilseed rape, thereby decreasing the ability to transport Cd [51]. Ethanol-extractable Cd represents inorganic water-soluble Cd, including nitrate/nitrite, chloride, and aminophenol Cd [58]. Our study found that 1–100 μM concentrations of MeJA significantly enhanced ethanol-extractable Cd compared with Cd treatment alone, suggesting that much Cd existed in its basic form. In a previous study, MeJA induced the genes encoding caffeic acid *O*-methyltransferase (*COMT*) [59], which is an important methylating enzyme in the phenylpropanoid pathway. The increased expression of *COMT* promoted the degree of lignification in tobacco (*Nicotiana tabacum*) [60]. It could be concluded that 1–100 μM MeJA may induce the expression of genes related to lignin deposition, increase the degree of lignification, and thus prevent Cd from becoming extracellular. Above all, lower concentrations of MeJA strengthened the tolerance of *C. bipinnatus* mainly through enhancing the Cd capacity of the CW, while higher MeJA concentrations may have induced an increase in the degree of lignification causing Cd obstruction.

MeJA affected antioxidant systems

Plants under environmental stress accumulate ROS, which can disturb plant metabolic systems [61]. Plants have accordingly evolved various antioxidant systems to eliminate oxidative stress [45]. It has been shown that MeJA can affect the activity of antioxidant enzymes, thereby relieving oxidative stress [47]. Application of MeJA to salt-stressed *Nitraria tangutorum* resulted in its SOD and CAT enzyme contents, which further activated the antioxidant defenses of *Nitraria tangutorum* seedlings [62]. Similarly, in the present study, MeJA affected the activity of antioxidant enzymes. High-concentration MeJA treatments significantly enhanced SOD activity compared with Cd treatment alone, indicating that the high concentration of MeJA disturbed the balance of antioxidant enzyme systems in plants (Fig. 5-B) [63]. These results indicated that MeJA may regulate the activity levels of different enzymes to protect *C. bipinnatus* under Cd stress, and exogenous MeJA with an appropriate concentration can alleviate damage caused by Cd (Fig. 10).

MeJA affected the absorption of cd by altering RCW polysaccharides

During plant growth, the symplast and apoplast pathways are the main modes of short-distance transport in plants, through which plants transport water and ions for their normal growth [64]. The symplast pathway uses intercellular junctions as bridges from one cell to another, whereas the apoplast pathway transmits materials through the CW and the free space within the cell interstitial space. In our study, Cd uptake through the apoplast pathway was much higher than that through the symplast pathway under all treatments. The Cd content in both the apoplast and symplast was decreased by the addition of exogenous MeJA, and apoplast Cd content

was significantly reduced under low concentrations of MeJA, which suggested that MeJA reduced the uptake of Cd by regulating the lateral transport in the plant, thus alleviating Cd toxicity. In contrast, in the apoplast pathway, although the CW is not part of the extracellular space, the structure of the CW has great influence on the extracellular space, and it plays an important role in alleviating heavy metal stress [32]. The CW is an indispensable part of plant cells, and it can determine the shape and volume of cells and act as a mechanical support and physical barrier for plants. The CW is able to respond to changes in the external environment by changing its own composition and structure, so as to improve the resistance of plants to various stress conditions [32]. Among them, polysaccharides, as the main components of plant CW, have various reactive groups to adsorb and immobilize Cd, and thus are important binding sites for heavy metals [15, 65]. Under Cd stress, the contents of P, HC1 and HC2, were increased in the roots of *Solanum nigrum*, which enhanced the tolerance of *S. nigrum* to Cd [10]. In our study, under Cd treatment alone, HC1 and P were the main Cd-binding polysaccharides in the RCW of *C. bipinnatus* (Fig. 7). Additionally, low-concentration MeJA treatment significantly increased the content of HC1 and the combined amount of Cd in HC1 and P fractions. It is possible that exogenous MeJA could change the structure of P and HC in the RCW, such that they can increase in the amount of Cd bound to the CW, promote the immobility of Cd, and decrease the Cd translocation factors (Fig. 2-C) [66]. This is also consistent with the findings of Zhang et al. [67] that externally applied low concentrations of MeJA under Cd stress increased the P, HC1 and HC2 contents of wheat CWs, thereby significantly improving the tolerance of wheat to Cd.

The polysaccharides in plant CW contain hydroxyl (-OH), carboxyl (-COOH), and amino groups ($-NH_2$), the adsorption of these groups can alter the occurrence and migration of Cd in the plant, thus reducing the toxicity of Cd to plants [68]. The identity of each functional group can be determined by the offset of the peak value of each functional group from plant samples grown under each treatment in the FTIR spectrum. Peaks near the 3400 cm^{-1} wavenumber correspond to the superposition of hydroxyl group (-OH), amino acid, and protein amino group (N-H) stretching vibration peaks, which mainly indicate the contribution of P, cellulose, hemicelluloses, and other polysaccharides in plant tissues to the spectrum [69]. Near 2920 cm^{-1} and 1060 cm^{-1} were found the stretching vibration absorption peaks of alkyl C-H and C-O groups, respectively, of cellulose, hemicellulose, and lignin [70]. The stretching vibration peak of protein amide (C-N) was near 1640 cm^{-1}, which is the characteristic absorption peak of protein. The C-H deformation vibration of cellulose and hemicellulose was generated near 1370 cm^{-1}. In our study, under Cd stress, the absorption peak of the characteristic hydroxyl (-OH) group peak (3420 cm^{-1}) and methyl ($-CH_3$) peak (2920 cm^{-1}) moved to low frequencies compared with the blank control group (Fig. 9-A), which was similar to the findings of Yu et al. [69]. This indicated high-concentration Cd stress led to the hydroxyl (-OH) group and the methyl ($-CH_3$) group peaks shifting together [71]. At the same time, these findings also showed that hydroxyl (-OH) was an important functional group for Cd adsorption. After MeJA application, the absorption peaks of ester groups (C=O) at 1720 cm^{-1} all shifted, indicating that under MeJA treatment, the methyl esterification degree of P in the *C. bipinnatus* RCW decreased, which increased the content of negatively charged free carboxyl (-COOH) groups and enhanced the adsorption capacity of Cd. This mechanism made Cd more easily combine with the RCW and impeded its transport to the aboveground shoots, which was also consistent with our findings (Fig. 2). Thus, it can be inferred that when exogenous MeJA is applied at a certain concentration to *C. bipinnatus* under Cd stress, plants can continuously improve their ability to adapt to Cd stress by regulating the contents of polysaccharides, proteins, and other substances as well as functional groups such as hydroxyl (-OH) and carboxyl (-COOH) groups (Fig. 10).

Conclusion

In the present study, Cd stress on *C. bipinnatus* was affected by the addition of different concentrations of exogenous MeJA. Specifically, exogenous MeJA affected Cd uptake and transport by *C. bipinnatus* by altering the polysaccharide composition, Cd subcellular distribution, and chemical form of *C. bipinnatus* in the RCW. Additionally, the activity of antioxidant enzymes was significantly enhanced by low concentrations of MeJA, which improved the resistance of *C. bipinnatus* seedlings to Cd toxicity. The above results suggest that treatment with appropriate MeJA concentrations can help activate protective mechanisms in plants. Overall, this study provides new insights into the utilization of exogenous MeJA to mitigate heavy metal toxicity and indicates the potential value of the novel application of MeJA for bioremediation of Cd pollution. Finally, this result can help to further explore the related process of MeJA regulation of CW synthesis and the associated changes in gene expression, which will lay the foundation for future applications of phytohormones to mitigate plant stress.

Abbreviations

Ar	Arsenic
AsA	Ascorbic acid
Cav	*C. bipinnatus Cosmos bipinnatus*
CAT	Catalase
Cd	Cadmium
COMT	Catechol-*O*-methyltransferase

Cu	Copper
CW	Cell wall
FTIR	Fourier transform infrared spectroscopy
GPI	Glycosylphosphatidylinositol
GSH	Glutathione
HAC	Acetic acid
HC1	Hemicellulose 1
HC2	Hemicellulose 2
JA	Jasmonic acid
MDA	Malondialdehyde
MeJA	Methyl jasmonate
N.D.	Not detected
N.S.	Not significant
NBT	Nitroblue tetrazolium
P	Pectin
PME	Pectin methylesterase
POD	Peroxidase
RCW	Root cell wall
ROS	Reactive oxygen species
SOD	Superoxide dismutase
TF	Translocation factor
XTH	Xyloglucan endotransglucosylase/hydrolase

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-024-05526-2.

Supplementary Material 1

Author contributions

Conceptualization: Xiaofang Yu, Yujia Liu and Liu Yang. Formal analysis: Yujing Liu, Chunyu Fan, Zihan Yang, Yuhan Xu and Xiaoxuan Zeng. Writing-original draft preparation: Xiaofang Yu, Yujia Liu and Liu Yang. Review and provided valuable suggestions: Xue Xiao, Lijuan Yang, Ting Lei, Mingyan Jiang, Xi Li, Suping Gao and Qi Tao. Funding acquisition: XiaoFang Yu. All authors have read and agreed to the published version of the manuscript. The diagram of Cosmos bipinnatus Cav. used in this graphical abstract has been reproduced with permission from Chunyu Fan.

Funding

The authors would like to thank the National Natural Science Foundation of China (grant no.22206140).

Data availability

All data generated or analyzed during this study are included in this published article.

Declarations

Ethics approval and consent to participate

We all declare that the study reported in this manuscript did not involve any human participants, human data, or human tissue, so this is not applicable.

Consent for publication

Not applicable.

Experimental research and field studies on plants (either cultivated or wild), including the collection of plant material, must comply with relevant institutional, national, and international guidelines and legislation

We confirm that all methods were performed in accordance with the relevant guidelines/regulations/legislation.

Competing interests

The authors declare no competing interests.

Received: 10 May 2024 / Accepted: 20 August 2024
Published online: 27 August 2024

References

1. Zhang X, Yang M, Yang H, Pian R, Wang J, Wu A-M. The uptake, transfer, and detoxification of cadmium in plants and its exogenous effects. Cells. 2024;13(11):907.
2. Ismael MA, Elyamine AM, Moussa MG, Cai M, Zhao X, Hu C. Cadmium in plants: uptake, toxicity, and its interactions with selenium fertilizers. Metallomics. 2019;11(2):255–77.
3. Miclean M, Cadar O, Levei EA, Roman R, Ozunu A, Levei L, Metal. (Pb, Cu, Cd, and zn) transfer along food chain and health risk assessment through raw milk consumption from free-range cows. Int J Env Res Public Health. 2019;16(21):4064.
4. Benton MA, Rager JE, Smeester L, Fry RC. Comparative genomic analyses identify common molecular pathways modulated upon exposure to low doses of arsenic and cadmium. BMC Genomics. 2011;12:1–10.
5. Amjadi Z, Namdjoyan S, Abolhasani Soorki A. Exogenous melatonin and salicylic acid alleviates cadmium toxicity in safflower (Carthamus tinctorius L.) seedlings. Ecotoxicology. 2021;30:387–401.
6. Meng Y, Jing H, Huang J, Shen R, Zhu X. The role of nitric oxide signaling in plant responses to cadmium stress. Int J Mol Sci. 2022;23(13):6901.
7. Zhu T, Li L, Duan Q, Liu X, Chen M. Progress in our understanding of plant responses to the stress of heavy metal cadmium. Plant Signal Behav. 2021;16(1):1836884.
8. Zhan J, Huang H, Yu H, Zhang X, Zheng Z, Wang Y, Liu T, Li T. The combined effects of cd and pb enhanced metal binding by root cell walls of the phytostabilizer Athyrium Wardii (Hook). Environ Pollut. 2020;258:113663.
9. Vázquez S, Goldsbrough P, Carpena R. Assessing the relative contributions of phytochelatins and the cell wall to cadmium resistance in white lupin. Physiol Plant. 2006;128(3):487–95.
10. Wang J, Chen X, Chu S, Hayat K, Chi Y, Zhi Y, Zhang D, Zhou P. Influence of cd toxicity on subcellular distribution, chemical forms, and physiological responses of cell wall components towards short-term cd stress in Solanum nigrum. Environ Sci Pollut Res. 2021;28:13955–69.
11. Dora S, Terrett OM, Sánchez-Rodríguez C. Plant–microbe interactions in the apoplast: communication at the plant cell wall. Plant Cell. 2022;34(5):1532–50.
12. Huang WX, Chen XW, Wu L, Yu ZS, Gao MY, Zhao HM, Mo CH, Li YW, Cai QY, Wong MH. Root cell wall chemistry remodelling enhanced arsenic fixation of a cabbage cultivar. J Hazard Mater. 2021;420:126165.
13. Zhang S, Sun Z, Zheng T, He C, Lin D. Nanoplastics increase algal absorption and toxicity of cd through alterations in cell wall structure and composition. Water Res. 2024;254:121394.
14. Yu H, Wu Y, Huang H, Zhan J, Wang K, Li T. The predominant role of pectin in binding cd in the root cell wall of a high cd accumulating rice line (Oryza sativa L). Ecotoxicol Environ Saf. 2020;206:111210.
15. Ren C, Qi Y, Huang G, Yao S, You J, Hu H. Contributions of root cell wall polysaccharides to Cu sequestration in castor (Ricinus communis L.) exposed to different Cu stresses. J Environ Sci. 2020;88:209–16.
16. Jeyasri R, Muthuramalingam P, Karthick K, Shin H, Choi SH, Ramesh M. Methyl jasmonate and salicylic acid as powerful elicitors for enhancing the production of secondary metabolites in medicinal plants: an updated review. Plant Cell, Tissue Organ Cult. 2023, 153(3):447–458.
17. Li X, Wang Z, Sun S, Dai Z, Zhang J, Wang W, Peng K, Geng W, Xia S, Liu Q. IbNIEL-mediated degradation of IbNAC087 regulates jasmonic acid-dependent salt and drought tolerance in sweet potato. J Integr Plant Biol. 2024;66(2):176–95.
18. Yu X, Zhang W, Zhang Y, Zhang X, Lang D, Zhang X. The roles of methyl jasmonate to stress in plants. Funct Plant Biol. 2018;46(3):197–212.
19. SÁNCHEZ-ROMERA B, RUIZ-LOZANO JM, Li G, LUU DT, MARTÍNEZ-BALLESTA MDC, Carvajal M, Zamarreño AM, GARCÍA-MINA JM, Maurel C, Aroca R. Enhancement of root hydraulic conductivity by methyl jasmonate and the role of calcium and abscisic acid in this process. Plant Cell Environ. 2014;37(4):995–1008.
20. Ismail A, Riemann M, Nick P. The jasmonate pathway mediates salt tolerance in grapevines. J Exp Bot. 2012;63(5):2127–39.
21. Wu H, Ye H, Yao R, Zhang T, Xiong L. OsJAZ9 acts as a transcriptional regulator in jasmonate signaling and modulates salt stress tolerance in rice. Plant Sci. 2015;232:1–12.
22. He Q, Hong K, Zou R, Liao F, Cui S, Zhang E, Huang M. The role of jasmonic acid and lipoxygenase in propylene-induced chilling tolerance on banana fruit. Eur Food Res Technol. 2014;238:71–8.
23. Siboza XI, Bertling I, Odindo AO. Salicylic acid and methyl jasmonate improve chilling tolerance in cold-stored lemon fruit (Citrus limon). J Plant Physiol. 2014;171(18):1722–31.

24. Yan Z, Li X, Chen J, Tam NF-Y. Combined toxicity of cadmium and copper in Avicennia marina seedlings and the regulation of exogenous jasmonic acid. Ecotoxicol Environ Saf. 2015;113:124–32.
25. Yan Z, Zhang W, Chen J, Li X. Methyl jasmonate alleviates cadmium toxicity in Solanum nigrum by regulating metal uptake and antioxidative capacity. Biol Plant. 2015;59(2):373–81.
26. Scognamiglio J, Jones L, Letizia C, Api A. Fragrance material review on methyl jasmonate. Food Chem Toxicol. 2012;50:S572–6.
27. Chen J, Yan Z, Li X. Effect of methyl jasmonate on cadmium uptake and antioxidative capacity in Kandelia obovata seedlings under cadmium stress. Ecotoxicol Environ Saf. 2014;104:349–56.
28. Farooq MA, Gill RA, Islam F, Ali B, Liu H, Xu J, He S, Zhou W. Methyl jasmonate regulates antioxidant defense and suppresses arsenic uptake in Brassica napus L. Front. Plant Sci. 2016;7:468.
29. Cao S, Zheng Y, Wang K, Rui H, Tang S. Effect of methyl jasmonate on cell wall modification of loquat fruit in relation to chilling injury after harvest. Food Chem. 2010;118(3):641–7.
30. Du J, Zeng J, Ming X, He Q, Tao Q, Jiang M, Gao S, Li X, Lei T, Pan Y. The presence of zinc reduced cadmium uptake and translocation in Cosmos bipinnatus seedlings under cadmium/zinc combined stress. Plant Physiol Biochem. 2020;151:223–32.
31. Liu Y, Yu X, Feng Y, Zhang C, Wang C, Zeng J, Huang Z, Kang H, Fan X, Sha L. Physiological and transcriptome response to cadmium in cosmos (Cosmos bipinnatus Cav.) Seedlings. Sci Rep. 2017;7(1):14691.
32. Yu X, Yang L, Fan C, Hu J, Zheng Y, Wang Z, Liu Y, Xiao X, Yang L, Lei T. Abscisic acid (ABA) alleviates cadmium toxicity by enhancing the adsorption of cadmium to root cell walls and inducing antioxidant defense system of Cosmos bipinnatus. Ecotoxicol Environ Saf. 2023;261:115101.
33. Dai H, Wei S, Twardowska I, Han R, Xu L. Hyperaccumulating potential of Bidens pilosa L. for cd and elucidation of its translocation behavior based on cell membrane permeability. Environ Sci Pollut Res. 2017;24:23161–7.
34. Su Y, Liu J, Lu Z, Wang X, Zhang Z, Shi G. Effects of iron deficiency on subcellular distribution and chemical forms of cadmium in peanut roots in relation to its translocation. Environ Exp Bot. 2014;97:40–8.
35. Wang X, Liu Y, Zeng G, Chai L, Song X, Min Z, Xiao X. Subcellular distribution and chemical forms of cadmium in Bechmeria Nivea (L.) Gaud. Environ Exp Bot. 2008;62(3):389–95.
36. Wang P, Deng X, Huang Y, Fang X, Zhang J, Wan H, Yang C. Comparison of subcellular distribution and chemical forms of cadmium among four soybean cultivars at young seedlings. Environ Sci Pollut Res. 2015;22:19584–95.
37. Knörzer OC, Burner J, Boger P. Alterations in the antioxidative system of suspension-cultured soybean cells (Glycine max) induced by oxidative stress. Physiol Plant. 1996;97(2):388–96.
38. Giannopolitis CN, Ries SK. Superoxide dismutases: I. occurrence in higher plants. Plant Physiol. 1977;59(2):309–14.
39. Han S, Chen L-S, Jiang H-X, Smith BR, Yang L-T, Xie C-Y. Boron deficiency decreases growth and photosynthesis, and increases starch and hexoses in leaves of citrus seedlings. J Plant Physiol. 2008;165(13):1331–41.
40. de Azevedo Neto AD, Prisco JT, Enéas-Filho J, de Abreu CEB, Gomes-Filho E. Effect of salt stress on antioxidative enzymes and lipid peroxidation in leaves and roots of salt-tolerant and salt-sensitive maize genotypes. Environ Exp Bot. 2006;56(1):87–94.
41. Redjala T, Sterckeman T, Skiker S, Echevarria G. Contribution of apoplast and symplast to short term nickel uptake by maize and leptoplax emarginata roots. Environ Exp Bot. 2010;68(1):99–106.
42. Zhu XF, Lei GJ, Jiang T, Liu Y, Li GX, Zheng SJ. Cell wall polysaccharides are involved in P-deficiency-induced cd exclusion in Arabidopsis thaliana. Planta. 2012;236:989–97.
43. Yang JL, Zhu XF, Peng YX, Zheng C, Li GX, Liu Y, Shi YZ, Zheng SJ. Cell wall hemicellulose contributes significantly to aluminum adsorption and root growth in Arabidopsis. Plant Physiol. 2011;155(4):1885–92.
44. Li W, Ullah S, Xu Y, Bai T, Ye S, Jiang W, Yang M. Effects of elevated aluminum concentration and distribution on Root damage, Cell Wall Polysaccharides, and nutrient uptake in different tolerant Eucalyptus clones. Int J Mol Sci. 2022;23(21):13438.
45. Yu X, Yang Z, Xu Y, Wang Z, Fan C, Zeng X, Liu Y, Lei T, Jiang M, Li J. Effect of chromium stress on metal accumulation and cell wall fractions in Cosmos bipinnatus. Chemosphere. 2023;315:137677.
46. Kolupaev YE, Yastreb TO, Dmitriev AP. Signal mediators in the implementation of jasmonic acid's protective effect on plants under abiotic stresses. Plants 2023, 12(14):2631.
47. Yan Z, Chen J, Li X. Methyl jasmonate as modulator of cd toxicity in Capsicum frutescens var. Fasciculatum seedlings. Ecotoxicol Environ Saf. 2013;98:203–9.
48. Ning Y, Ding Y-k, Chang Y-h, Zhang S, An H-m. Fu Y-j. Low concentration of MeJA-elicited the positive growth of Rosa roxburghii via balancing phytohormone signal transduction and triterpenoids synthesis. Plant Growth Regul. 2023;101(1):187–99.
49. Fahad S, Hussain S, Saud S, Hassan S, Ihsan Z, Shah AN, Wu C, Yousaf M, Nasim W, Alharby H. Exogenously applied plant growth regulators enhance the morpho-physiological growth and yield of rice under high temperature. Front Plant Sci. 2016;7:1250.
50. Bai X, Dong Y, Kong J, Xu L, Liu S. Effects of application of salicylic acid alleviates cadmium toxicity in perennial ryegrass. Plant Growth Regul. 2015;75:695–706.
51. Qiu Q, Wang Y, Yang Z, Yuan J. Effects of phosphorus supplied in soil on subcellular distribution and chemical forms of cadmium in two Chinese flowering cabbage (Brassica parachinensis L.) cultivars differing in cadmium accumulation. Food Chem Toxicol. 2011;49(9):2260–7.
52. van de Meene A, McAloney L, Wilson SM, Zhou J, Zeng W, McMillan P, Bacic A, Doblin MS. Interactions between Cellulose and (1, 3; 1, 4)-β-glucans and Arabinoxylans in the Regenerating Wall of Suspension Culture Cells of the Ryegrass Lolium multiflorum. Cells. 2021, 10(1):127.
53. Martinka M, Vaculík M, Lux A. Plant cell responses to cadmium and zinc. Applied Plant Cell Biology: Cellular Tools and Approaches for Plant Biotechnology 2014:209–246.
54. Adamczyk-Szabela D, Chrześcijańska E, Zielenkiewicz P, Wolf WM. Antioxidant activity and photosynthesis efficiency in Melissa officinalis Subjected to Heavy metals stress. Molecules. 2023;28(6):2642.
55. Yu X-F, Wang Z-W, Chen F-L, Chen M-L, Zhang X-Y, Zhang J-R, Ji W-Y, Xiao X, Yang L-J, Lei T. The mitigation of citric acid on cadmium toxicity in Iris tectorum and its effects on the composition of cell walls. Int Biodeterior Biodegrad. 2024;193:105857.
56. Wei T, Li X, Yashir N, Li H, Sun Y, Hua L, Ren X, Guo J. Effect of exogenous silicon and methyl jasmonate on the alleviation of cadmium-induced phytotoxicity in tomato plants. Environ Sci Pollut Res. 2021;28:51854–64.
57. Paynel F, Schaumann A, Arkoun M, Douchiche O, Morvan C. Temporal regulation of cell-wall pectin methylesterase and peroxidase isoforms in cadmium-treated flax hypocotyl. Ann Bot. 2009;104(7):1363–72.
58. Luo J, Feng S, Li M, He Y, Deng Y, Cao M. Effect of magnetized water irrigation on cd subcellular allocation and chemical forms in leaves of Festuca arundinacea during phytoremediation. Ecotoxicol Environ Saf. 2024;277:116376.
59. Lee JE, Vogt T, Hause B, Löbler M. Methyl jasmonate induces an O-Methyltransferase in barley1. Plant Cell Physiol. 1997;38(7):851–62.
60. Sewalt VJ, Ni W, Blount JW, Jung HG, Masoud SA, Howles PA, Lamb C, Dixon RA. Reduced lignin content and altered lignin composition in transgenic tobacco down-regulated in expression of L-phenylalanine ammonia-lyase or cinnamate 4-hydroxylase. Plant Physiol. 1997;115(1):41–50.
61. Panda SK, Gupta D, Patel M, Vyver CVD, Koyama H. Functionality of Reactive Oxygen Species (ROS) in Plants: Toxicity and Control in Poaceae Crops Exposed to Abiotic Stress. Plants. 2024, 13(15):2071.
62. Gao Z, Gao S, Li P, Zhang Y, Ma B, Wang Y. Exogenous methyl jasmonate promotes salt stress-induced growth inhibition and prioritizes defense response of Nitraria Tangutorum Bobr. Physiol Plant. 2021;172(1):162–75.
63. Shi G, Xia S, Liu C, Zhang Z. Cadmium accumulation and growth response to cadmium stress of eighteen plant species. Environ Sci Pollut Res. 2016;23:23071–80.
64. Pan T, Dong Q, Cai Y, Cai K. Silicon-mediated regulation of cadmium transport and activation of antioxidant defense system enhances Pennisetum glaucum resistance to cadmium stress. Plant Physiol Biochem. 2023;195:206–13.
65. Tkalec M, Štefanić PP, Cvjetko P, Šikić S, Pavlica M, Balen B. The effects of cadmium-zinc interactions on biochemical responses in tobacco seedlings and adult plants. PLoS ONE. 2014;9(1):e87582.
66. Lasat MM, Baker AJ, Kochian LV. Altered zn compartmentation in the root symplasm and stimulated zn absorption into the leaf as mechanisms involved in Zn hyperaccumulation in Thlaspi caerulescens. Plant Physiol. 1998;118(3):875–83.
67. Zhang D, Wang H, Zhang Y, Su Z, Hu T, Liu J, Ding Q, Niu N, Ma L. Methyl jasmonate enhances the safe production ability of Cd-stressed wheat by regulating the antioxidant capacity, cd absorption, and distribution in wheat. Plant Physiol Biochem. 2024:108788.
68. Cao S, Pan J, Rehman M, Luo D, Wang Q, Jin G, Li R, Chen T, Chen P. Exogenous nitric oxide alleviates cadmium toxicity in kenaf (Hibiscus cannabinus

L.) through modulating cd deposition and regulating key genes and involved pathways. Ind Crops Prod. 2024;221:119359.
69. Azuma W, Nakashima S, Yamakita E, Ishii HR, Kuroda K. Water retained in tall Cryptomeria japonica leaves as studied by infrared micro-spectroscopy. Tree Physiol. 2017;37(10):1367–78.
70. Chen X, Zhang Q, Achal V. Adsorption of metals by watermelon-peel-derived biochar and mechanism in aqueous solution. J Environ Eng Sci. 2020;15(3):99–106.
71. Yu S, Sheng L, Mao H, Huang X, Luo L, Li Y. Physiological response of Conyza Canadensis to cadmium stress monitored by Fourier transform infrared spectroscopy and cadmium accumulation. Spectrochim Acta Part A Mol Biomol Spectrosc. 2020;229:118007.

Publisher's note