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RESEARCH ARTICLE

Alleviation of Cd phytotoxicity and enhancement of rape seedling growth by plant growth–promoting bacterium *Enterobacter* sp. Zm-123

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Abstract

The present study aims to investigate the impact of a metal-tolerant bacterium on metal detoxification and rape seedling growth promotion under Cd stress. The results showed that the isolated bacterium *Enterobacter* sp. Zm-123 has capability to resist Cd (200 mg/L), produce IAA (26.67 mg/L) and siderophores (82.34%), and solubilize phosphate (137.5 mg/L), etc. Zm-123 inoculation significantly enhanced the fresh weight of rape seedlings from 9.47 to 19.98% and the root length from 10.42 to 57.05% compared with non-inoculation group under different concentrations of Cd (0, 0.5, 1, 3, 5 mg/L) ($p < 0.05$). It also significantly increased the content of chlorophyll, soluble sugar, soluble protein, and proline ($p < 0.05$) in rape seedlings. Moreover, a significant elevation in catalase (CAT) and peroxidase (POD) activities and a significant reduction in malondialdehyde (MDA), electrolyte leakage (EL), and Cd content in rape seedlings were detected owing to Zm-123 inoculation ($p < 0.05$). The combined results imply that strain Zm-123 can alleviate the Cd phytotoxicity and promote the rape seedling growth by improving the physiological activity and antioxidant level, which can be potentially applied to protect plants from Cd toxicity.

Keywords Cadmium · Plant growth–promoting activity · Rape seedlings · *Enterobacter* sp. Zm-123

Introduction

Along with the phosphate fertilizer application, sewage irrigation, and mining waste emission, a large amount of cadmium (Cd) has been introduced into soil, endangering food safety and human health (Shahid et al. 2016). Cd can be readily absorbed by the roots and transported to the shoots, leading to Cd accumulation in the edible parts of plants and forming a primary source of dietary Cd intake (Podazza et al. 2012). It has been reported that 72% of Cd in the daily diet of human comes from vegetables (Baldantoni et al. 2016). Cd may also deteriorate plant quality, such as slowing down the seed germination, inhibiting the root elongation, etiolating the leaves, and reducing the plant biomass (Tran and Popova 2013). These adverse impacts have been attributed to interference on plant growth and physiology as well as oxidative stress of excess Cd, represented by the reduced content of soluble sugar and protein, the unspecific oxidation of proteins and membrane lipids, extracellular electrolyte leakage, and proline accumulation in plants (Andresen and Küpper 2013; Scandalios 2005; Xu et al. 2012). Thus, it is urgent to take effective measures for alleviating the Cd uptake and eliminating Cd toxicity in vegetable plants.

Microbe-assisted phytostabilization has been considered as an efficient strategy in eliminating metal toxicity to plants. Plant growth–promoting bacteria (PGPB), such as *Bacillus*, *Pseudomonas*, *Bradyrhizobium*, *Serratia*, and *Klebsiella*, have been reported to enhance plant growth and reduce metal toxicity through providing indoleacetic acid (IAA), siderophores, phosphate solubilization activity, etc.

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(Pramanik et al. 2017; Yu et al. 2018; Pandey et al. 2013). Bacterial IAA interferes with the physiological process of plants by changing the plant auxin pool, enlarging root surface area and length, and subsequently increasing the nutrient uptake Patten and Glick (2002), besides, it can detoxify Cd via enhancing the antioxidant capability of plants (Sinha and Mukherjee 2008; Rizvi et al. 2019; Ahmad et al. 2016). The phosphate-solubilizing ability of PGPB can assist host plants to assimilate more phosphate (Yu and Zhou 2009), while microbial siderophores can help plants to sequester irons and complex toxic metals (Glick 2012). Therefore, it is reasonable to speculate that PGPB, especially those with metal resistance, may promote plant growth and alleviate Cd toxicity under Cd stress.

Enterobacter spp. have been known to promote plant growth under drought, salinity, and metal stress by providing IAA, siderophore, ACC deaminase, and phosphate solubilization activity in wheat, rice, and maize, whereas there is no relevant report in rape. China has the longest history of rape production in the world, accounting for one-third of the world's rape planting area and total output (Liu et al. 2017; Yuan et al. 2020), while soil Cd pollution often causes Cd content in rapes exceeding the standard. Thus, the objectives of this study were (a) to evaluate the potential PGP characteristics and Cd tolerance ability of an isolated *Enterobacter* sp. and (b) to investigate the effects of these PGP characteristics on rape seedlings growth, physiological parameters, antioxidant capacity, and Cd uptake in edible parts under Cd stress using hydroponic culture system.

Materials and methods

Reagents

Cadmium chloride hemipentahydrate, copper sulfate pentahydrate, zinc nitrate hexahydrate, lead chloride, potassium dichromate, and other chemicals in analytical grade were purchased from Kermel Chemical Reagent Co., Ltd. (Tianjin, China).

Isolation and identification of Cd-tolerant bacteria

The rhizospheric soil for Cd-resistant bacteria isolation was taken from a mining area in the northeastern region of China. Ten grams of soil was transferred into a conical flask with 90-mL sterile distilled water and shaken in a rotator at 160 rpm and 28 °C for 30 min, then the obtained soil suspension was serially diluted (10^{-3}–10^{-5}) and an aliquot of 0.1 mL diluent was spread on Luria-Bertani agar medium supplied with 50 mg/L of Cd, and incubated at 28 °C for 3 days. The colonies on the medium plates were picked up and transferred several times to gain pure isolate. The physiological-biochemical characteristics of the isolate were determined according to "Bergey's Manual of Systematic Bacteriology." Besides, 16S rRNA gene was amplified using universal primer set f27 (5′-AGAGTTTGATCCTGGCTCAG-3′) and r1492 (5′-TACGGTTACCTTGTTACGACTT-3′) (Yu et al. 2018). The PCR products were sequenced by Meiji Biotech (Shanghai, China), and the acquired sequences were compared with those homologous sequences in GenBank. Phylogenetic tree of the isolate was obtained using neighbor-joining method of software packages Mega version 6.0 at a bootstrap value of $n = 1000$. To visualize the Cd cytotoxic damage on bacterial morphology, bacterium and metal-treated bacterium were subjected to TEM (model JSM 6510 LV; JEOL, Japan) analysis.

Heavy metal tolerance

Minimal inhibitory concentration (MIC) is the lowest metal concentration that can completely prevent bacterial growth and the maximum tolerant concentration (MTC) is the highest concentration of metal ion beyond which no visible bacteria growth occurred (Piotrowska-Seget et al. 2005). In this study, the MICs and MTCs of Cd(II), Pb(II), Zn(II), Cu(II), and Cr(VII) for the isolate were tested at a series of concentrations (100, 200, 300, 400, 600, 800, 1000 mg/L) on Luria-Bertani agar medium incubated at 30 °C for 3 days (Pramanik et al. 2016; Kumar et al. 2017).

Determination of growth curve

Growth curve of the isolate was determined with 100 mL of bacterial cultures (1×10^8 cells/mL in Luria-Bertani medium) supplemented with varying concentrations of Cd (0, 10, 20, 30, 40 and 50 mg/L) in 250-mL conical flasks. Flasks were kept in shaking condition at 30 °C for 28 h, and the optical density value was recorded at 600 nm every 2 h (Andrews 2001).

Selected PGP traits of the isolate

Indole acetic acid–producing ability

Production of indole acetic acid (IAA) by the isolate was quantified by spectrophotometric method as described by Clickmann et al. (Glickmann and Dessaux 1995). Briefly, 2 mL of the isolate suspension (10^8 cells/mL) was inoculated into 98 mL of Luria-Bertani medium with L-tryptophan (100 mg/L) and varying concentrations of Cd (0, 10, 20, 30, 40, and 50 mg/L). After 3 days, the amount of IAA in the filtrate was measured with a UV-Visible spectrophotometer (T6, Persee, China) at 540 nm and expressed as micrograms per milliliter of culture filtrate. Standard curve was plotted with chemical grade indole-3-acetic acid (Beijing Solarbio Science & Technology Co., Ltd., China).

Phosphate solubilization ability

Phosphate solubilization ability of the isolate was evaluated by cultivating the bacteria on agar-solidified Pikovskaya (PKO) medium at 30 °C for 5 days and measuring the diameter of the clear zone around the colony. Phosphate solubilization ability was also quantified after 2 mL of the isolate (1×10^8 cells/mL) was incubated in 98 mL PKO liquid medium containing varying concentrations of Cd (0, 10, 20, 30, 40, and 50 mg/L) at 180 rpm and 30 °C for 5 days (Chatterjee et al. 2012). The amount of soluble phosphate was measured colorimetrically after centrifugation of liquid cultures at 8000 rpm for 10 min (Ullah et al. 2013).

Siderophore-producing ability

Siderophore-producing ability of the isolate was detected using Chrome Azurol Sulphonate (CAS) medium at Cd concentrations of 0, 10, 20, 30, 40, and 50 mg/L referring to the method of Schwyn and Neilands (1987). Siderophore-producing ability was also quantified after 2 mL of the isolate (1×10^8 cells/mL) in 98 mL of LB liquid medium was incubated at 30 °C for 72 h. The supernatant was collected by centrifugation at 6000 rpm for 10 min, and then mixed with CAS solution at a ratio of 1:1. The siderophore content was calculated using the following formula: $SU\% = \frac{Ar-As}{Ar} \times 100\%$, where Ar is the absorbance of the non-bacterial group as reference and As is the absorbance of the sample at 630 nm.

Germination experiment

Seeds of rape (purchased from North Seed Industry Co., Ltd., China) were first rinsed with 75% (v/v) ethanol and sodium hypochlorite (3% v/v) for 3 min and then rinsed with sterile distilled water for three times. Twenty aseptic seeds were distributed at equal distances from each other on sterile filter papers in a sterilized Petri dish. A total of 10 mL of $CdCl_2$ solution (0, 10, 20, 30, 40, 50 mg/L) with 2 mL of bacterial suspension (1×10^8 cells/mL) was injected to per dish. The germination rate was calculated after 7 days' incubation at 28 °C according to formula (Vijayaragavan et al. 2011): $\text{Germination rate } (\%) = \frac{\text{The number of seeds germinated}}{\text{The total number of seeds tested.}} \times 100\%$.

Hydroponic experiment

The hydroponic nutrient solution was filter-sterilized with a 0.45-μm membrane filter (Sartorius Stedim Biotech, Germany) before use. A 4 weeks' hydroponic experiment was conducted to determine the effect of isolate on plant growth in a greenhouse (natural illumination, temperature between 24 and 30 °C, and the humidity remained at 65% ± 10%). After germination, the rape seedlings with the same growth rate were transplanted into a 1-L beaker containing Hoagland medium at Cd concentrations of 0, 0.5, 1, 3, and 5 mg/L. During the experiment, the Hoagland medium was replaced every 7 days accompanied with the addition of bacterial suspension (2 mL, 1×10^8 cells/mL) (Zhou et al. 2017; El-Nahrawy et al. 2019), and in the control group, bacterial suspension was replaced by an equivalent volume of sterile water. After 4 weeks of cultivation, the seedlings were harvested for physiochemical analysis and Cd content determination.

Measurement of physiological indexes of rape seedlings

Fresh weight and root length were measured at the end of the hydroponic experiment. The chlorophyll in the seedlings was extracted by ethanol and its total content was measured according to the method of Xu et al. (2018). MDA content was assayed based on the TBA-based colorimetric method described by Demiral and Ismail (2005). Electrolyte leakage (EL) was measured according to the method reported by Wang et al. (2008). Ten rinsed leaf discs were submerged in 10 mL of distilled water and then vacuumed for 10 min. The initial electrical conductivity was recorded as the EC1. The leaf tissues were heated at 100 °C for 20 min and cooled to room temperature for measuring the final electrical conductance (EC2). The percent EL was recorded using the following formula: $EL\,(\%) = \frac{EC1}{EC2} \times 100\%$. The catalase (CAT) activity was determined as described by Aebi (1984). The guaiacol peroxidase (POD) activity was determined as described by Khan et al. (2014). Proline content was determined according to the protocol of Bates et al. (1973). The extraction was done by sulfosalicylic acid and the absorbance values were recorded at 520 nm. The soluble protein and sugar content of the seedlings were measured following the method of Bradford (1976) and Jin et al. (2013), respectively. Cd content in plants was measured after 4 weeks according to the method of Fang et al. (2016). Briefly, edible parts were separated, weighed, and dried at 80 °C in an oven overnight. 0.1 g of dried samples was subjected to hotblock (180 °C) wet digestion by HNO_3 and HCl (v/v, 3/1). After digestion, the samples were cooled down and ultrapure water was added to get a final volume of 10.0 mL, then the Cd content in rape seedlings was measured by an atomic absorption spectrophotometer (AAS) (AA-6800, Shimadzu-GL, Japan).

Statistical analysis

All experiments were conducted in triplicate. Data were analyzed using SPSS 19.0 (SPSS Inc., USA) and expressed as means with their standard derivation (SD). The significant differences among the tested treatments were compared with Tukey's multiple comparisons test with $p < 0.05$ as a significant level.

Results

Identification of Zm-123 isolate

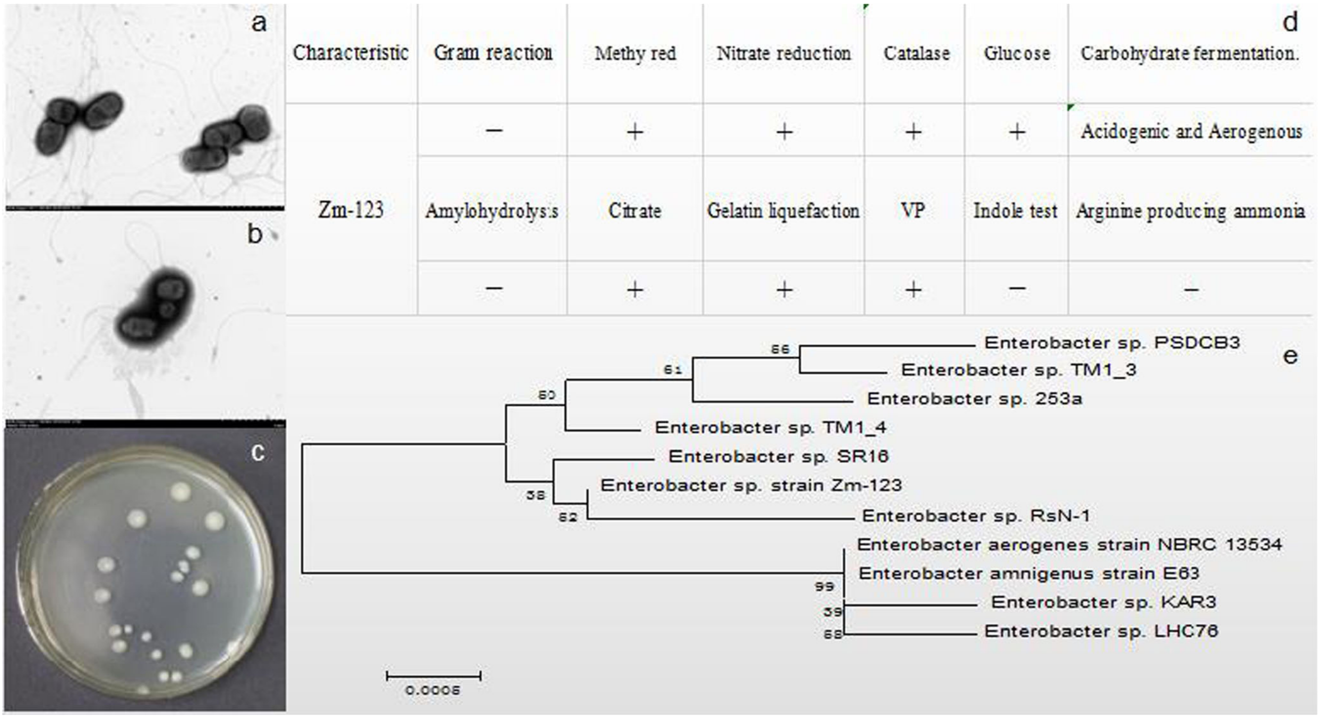
The isolated strain, designated as Zm-123, is an aerobic, motile, rod-shaped, flagellum-forming gram-negative bacterium (Fig. 1(a)). The morphology of Zm-123 treated with 30 mg/L Cd showed shrunken cell and distorted surface possibly with Cd depositions (Fig. 1(b)). The colony of Zm-123 on a solid medium plate is milky white, spherical, shiny, smooth, and raised (Fig. 1(c)). Physiology and biochemistry characteristics of the strain are shown in Fig. 1(d). The phylogenetic analysis of 16S rRNA gene sequence indicated that Zm-123 (GenBank accession number MN493849.1) belongs to the genus *Enterobacter* (Fig. 1(e)).

Heavy metal resistant ability

Lead, cadmium, zinc, chromium, and copper are the main heavy metals caused soil and water pollution in China. In this paper, the MICs of Pb(II), Cd(II), Zn(II), Cr(VII), and Cu(II) on Zm-123 were 600, 200, 200, 400, and 100 mg/L, respectively. The maximum tolerant concentrations of Pb(II), Cd(II), Zn(II), Cr(VII),and Cu(II) on Zm-123 were 1000, 600, 400, 800, and 300 mg/L (Table S1) indicating that Zm-123 has a high tolerance to multiple heavy metals.

Growth characteristics

From the growth curves shown in Fig. 2, it was noticed that Zm-123 experienced a rapid growth within 20 h and a slow growth from 20 to 30 h in the absence and presence of Cd. The maximum viable counts of bacteria decreased from 4.23×10^9 to 1.46×10^9 cfu/mL (the OD_{600} ranged from 1.94 to 0.98), when Cd concentration increased from 0 to 50 mg/L. The threshold of Cd^{2+} concentration was 20 mg/L, below which the growth of Zm-123 was similar to that of in the absence of Cd and above which significant growth inhibition was observed. Although the resistant strain had tolerance to heavy metals, higher concentrations of Cd inhibited the metabolism of bacterium and slowed down the propagation of Zm-123.



Characteristic	Gram reaction	Methy red	Nitrate reduction	Catalase	Glucose	Carbohydrate fermentation.
Zm-123	−	+	+	+	+	Acidogenic and Aerogenous
	Amylohydrolysis	Citrate	Gelatin liquefaction	VP	Indole test	Arginine producing ammonia
	−	+	+	+	−	−

Fig. 1 Morphology characteristics of native Zm-123 and 30-mg/L Cd-treated Zm-123 under TEM (× 6000) (a, b); colony characteristics of Zm-123 on a solid medium plate (c); physiology and biochemistry characteristics of Zm-123 (d); phylogenetic tree of Zm-123 at the bootstrap value of $n = 1000$ (e)

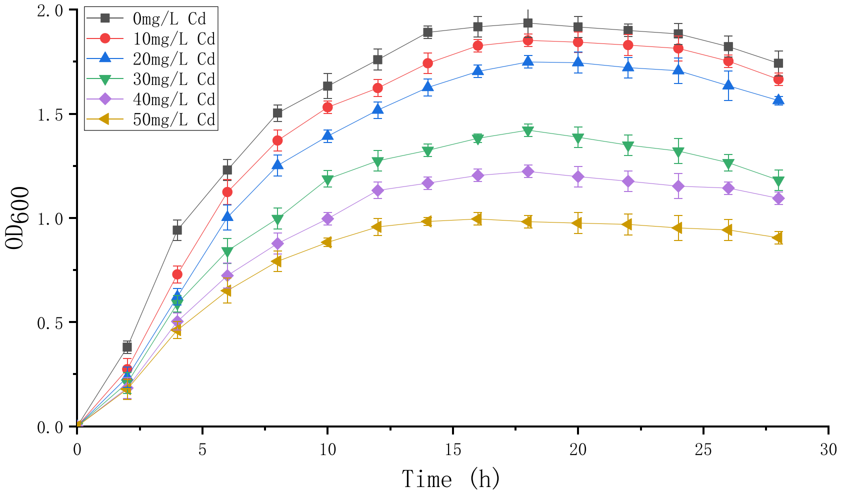


Fig. 2 Growth curve of Zm-123 at Cd concentrations of 0, 10, 20, 30, 40, and 50 mg/L

Growth-promoting activity

Low concentration of Cd could stimulate IAA production as seen in Fig. 3(a); the maximum IAA of 28.30 mg/L was detected at 5 mg/L of Cd, which was higher than that no Cd addition (26.67 mg/L). As the concentration exceeded 5 mg/L, the IAA production was constantly decreased to 25.4–20.1 mg/L. Zm-123 developed a clear halo zone around its colony after 72 h's incubation on PKO solid medium (Fig. S1a). As shown in Fig. S1b, the appearance of an orange halo around the colony on CAS agar plate indicated that Zm-123 produced siderophores. To further determine how Cd influences the selected important PGP traits, a quantitative test was conducted.

As shown in Fig. 3(b), phosphate solubilization was negatively affected by Cd concentration (Fig. 3(b)) and maximum phosphate of 137.50 mg/L was produced by strain Zm-123 in no Cd medium. Siderophore production of Zm-123 was decreased in a similar manner as seen in Fig. 3(c) and the maximum siderophore production (82.34% SU) was obtained in the absence of Cd. With the increment of Cd concentration, the siderophore production decreased significantly ($p < 0.05$), and it declined to a minimum of 10.78% SU at Cd concentration of 25 mg/L. The above results indicate that Zm-123 has plant growth–promoting ability.

Germination experiment

The effect of Zm-123 on the seed germination under Cd stress is shown in Table 1. Zm-123 treatment significantly improved the germination rate of rape seeds ($p < 0.05$) by 1.57% compared with that of the control group (93.66%). When the concentration of Cd was 10 mg/L, the germination rate of the Zm-123 treatment group was 2.01% higher than that of the non-treated group. As the concentration of Cd continued to increase, the germination rate decreased from 85.64 to 63.67% in the control group, while decreased from 89.42 to 78.78% in the Zm-123 group.

Hydroponics experiment

Measurement of growth and photosynthesis characteristics

Previous research showed that Cd might cause the leaf chlorosis and the chlorophyll damage, which resulted in growth retardation (Najeeb et al. 2011). In our hydroponics experiment, the presence of Cd in the nutrient solution caused decrement in fresh weight compared with that in the absence of Cd (Fig. 4(a)). However, the Zm-123-inoculated group increased the fresh weight by 12.18%,17.10%, 9.47%, 18.40%, and 19.98% and facilitated the root elongation by 37.5%, 10.83%, 18.45%, 15.48%, and 57.12% compared with the non-inoculated group at Cd concentrations of 0, 0.5, 1, 3, and 5 mg/L, respectively (Fig. 4(a, b)). Apparently, Cd played a dual role in enhancing or suppressing chlorophyll content; low level of Cd (0.5 mg/L) increased the total chlorophyll contents of seedlings, while high levels of Cd (1, 3 and 5 mg/L) decreased total chlorophyll contents. Zm-123 inoculation significantly ($p < 0.05$) increased total chlorophyll contents by 18.56%, 7.6%, 18.03%, and 96.67% at Cd concentrations of 0.5, 1, 3, and 5 mg/L, respectively (Fig. 4(c)).

MDA and EL levels in rape seedlings

Oxidative stress caused by Cd has been recognized as a key factor that inhibits plant growth (Andresen and Küpper 2013; Farooq et al. 2013). In the present study, it was found that the levels of MDA in rape seedlings were elevated by Cd. There was no significant difference in MDA levels between the Zm-123-inoculated and Zm-123-non-inoculated group without Cd stress, whereas inoculation triggered a significant reduction ($p < 0.05$) compared with non-inoculation under Cd stress. In detail, Zm-123 decreased MDA level by 21.75%,

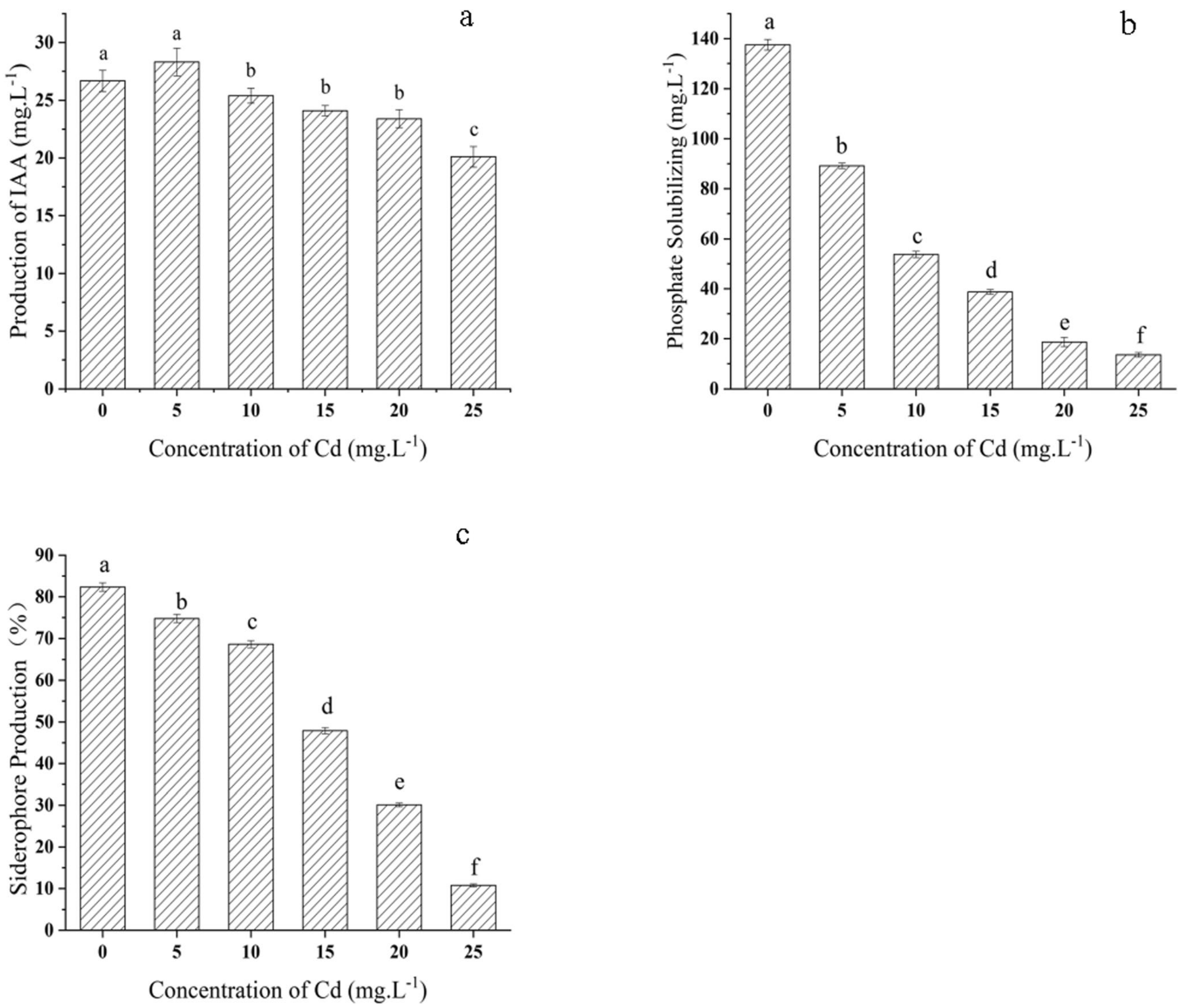


Fig. 3 Effect of different Cd concentrations on PGP traits of Zm-123: production of IAA (a), P-solubilization (b), and siderophore (c) production

28.61%, 13.68%, and 11.80% at Cd concentrations of 0.5, 1, 3, and 5 mg/L compared with that in the corresponding non-inoculated group, respectively (Fig. 5(a)). Cd toxicity further led to a substantial increase in the EL level of rape seedlings (Fig. 5(b)). These results suggested that Cd contamination triggered strong oxidative stress, while Zm-123 application significantly ($p < 0.05$) lowered EL in rape seedlings in the presence of 0.5, 1, 3, and 5 mg/L Cd than that without the Zm-123 group.

Table 1 Effect of Zm-123 on seed germination under different concentrations of Cd

Cd concentrations (mg/L)	Germination rate	
	CK	Zm-123
0	93.66% ± 2.11b	95.23% ± 1.69a
10	89.64% ± 1.46b	91.65% ± 2.51a
20	85.64% ± 1.67b	89.42% ± 3.37a
30	80.24% ± 2.52b	86.27% ± 1.95a
40	75.78% ± 2.16b	81.89% ± 2.67a
50	63.67% ± 1.36b	78.78% ± 1.78a

Different letters between the different treatment groups showed significant differences at the same Cd concentration ($p < 0.05$)

Antioxidant enzyme activities (CAT and POD)

Antioxidative enzymes such as CAT and POD are important to Cd damage control in plants (Xu et al. 2012). The variation of CAT activity and POD activity with the increasing concentration of Cd is depicted in Fig. 5(c, d). Under Cd stress (0.5 mg/L and 1 mg/L of Cd), CAT activity and POD activity were

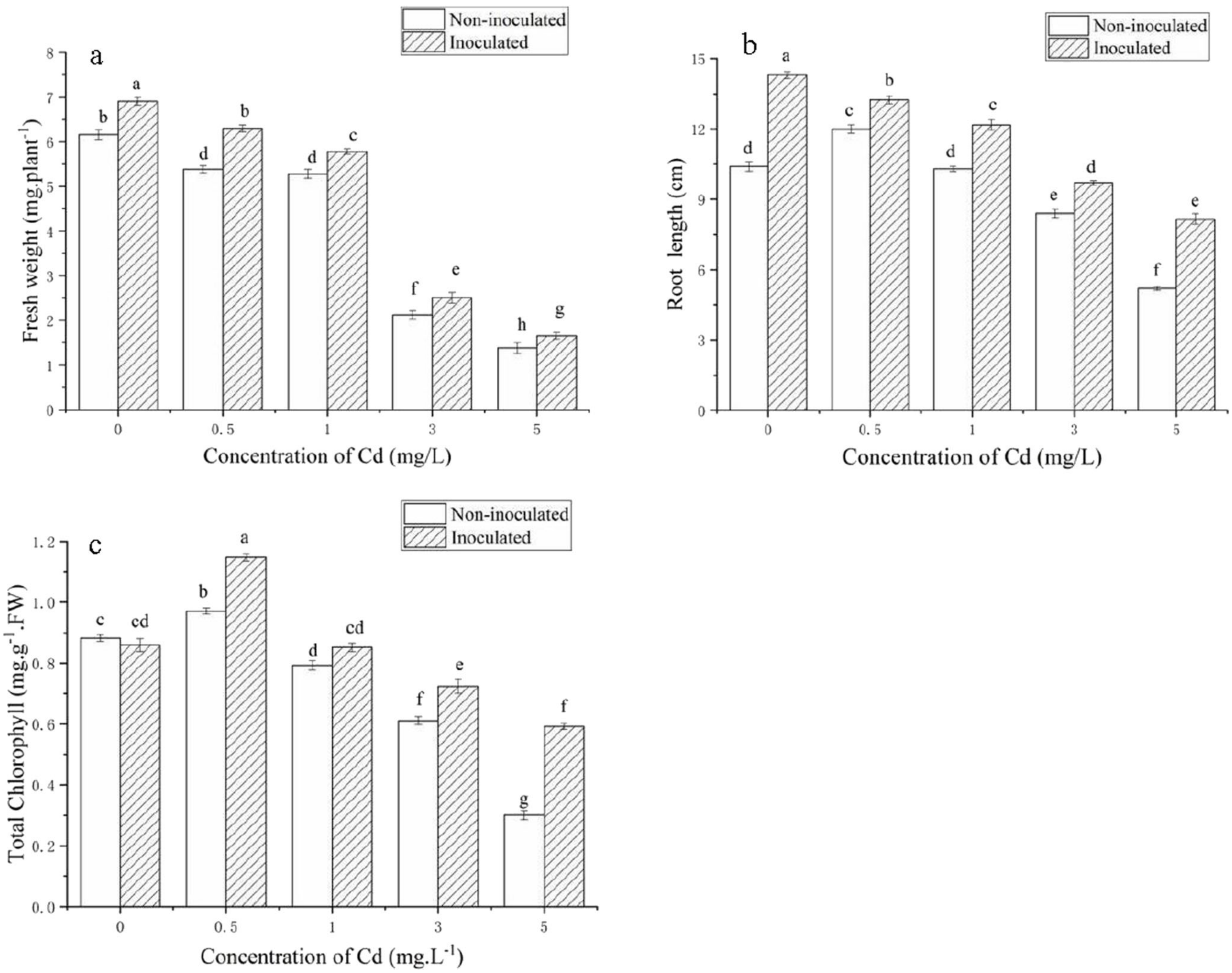


Fig. 4 Effects of Zm-123 inoculation on fresh weight (a), root length (b), and total chlorophyll in edible parts (c) of rape seedlings at different Cd concentrations after 4 weeks

significantly ($p < 0.05$) higher than that in unstressed. As Cd concentration increased from 0.5 to 5 mg/L, considerable decreases in the activities of CAT and POD were observed. The CAT activity in plants treated with Zm-123 was observed to be 10.53%, 12.12%, 22.34%, and 12.04% higher, respectively, at the 0.5, 1, 3, and 5 mg/L of Cd than that in the non-inoculated group. Similarly, POD activities in the Zm-123-inoculated group were higher than those in the non-inoculated group (Fig. 5(d)). Especially, a peak increase of 8.44% was obtained at 1 mg/L of Cd compared with that in non-inoculated.

Determination of proline, soluble sugar, and soluble protein contents in rape seedlings under Cd stress

Compared with the Cd-free group, proline contents were significantly elevated under Cd stress ($p < 0.05$). Inoculation of Zm-123 decreased proline contents compared with the non-inoculated groups under Cd stress. In detail, as Cd concentration increased from 0.5 to 5 mg/L, the proline content went up from 53.75 to 99.56 mg/g FW in non-inoculated and from 42.75 to 83.00 mg/g FW in the inoculated group, respectively. Especially, a great decrease (34.35%) was observed at 1 mg/L of Cd in contrast to the non-inoculated group. Soluble sugar, as energy and metabolic intermediates for plant growth and development and nutritional value for human beings, is greatly influenced by Cd (John et al. 2008). Without Zm-123 inoculation, the content of soluble sugar was enhanced from 3.01 to 10.63 mg/g FW as Cd concentration consistently increased from 0 to 1 mg/L, while decreased to 7.78 mg/g FW at Cd concentration of 5 mg/L. The addition of Zm-123 increased the content of soluble sugar by 40.00%, 19.57%, 11.21%, and 11.95% under the 0.5-, 1-, 3-, and 5-mg/L concentrations of Cd compared with the non-inoculated group, respectively (Fig. 6(b)). Considerable decreases in soluble protein contents were observed in the presence of Cd whereas Zm-123 inoculation significantly increased soluble protein contents in rape seedlings under Cd stress, and the maximum increment was obtained at Cd concentration of 1 mg/L. (Fig. 6(c)).

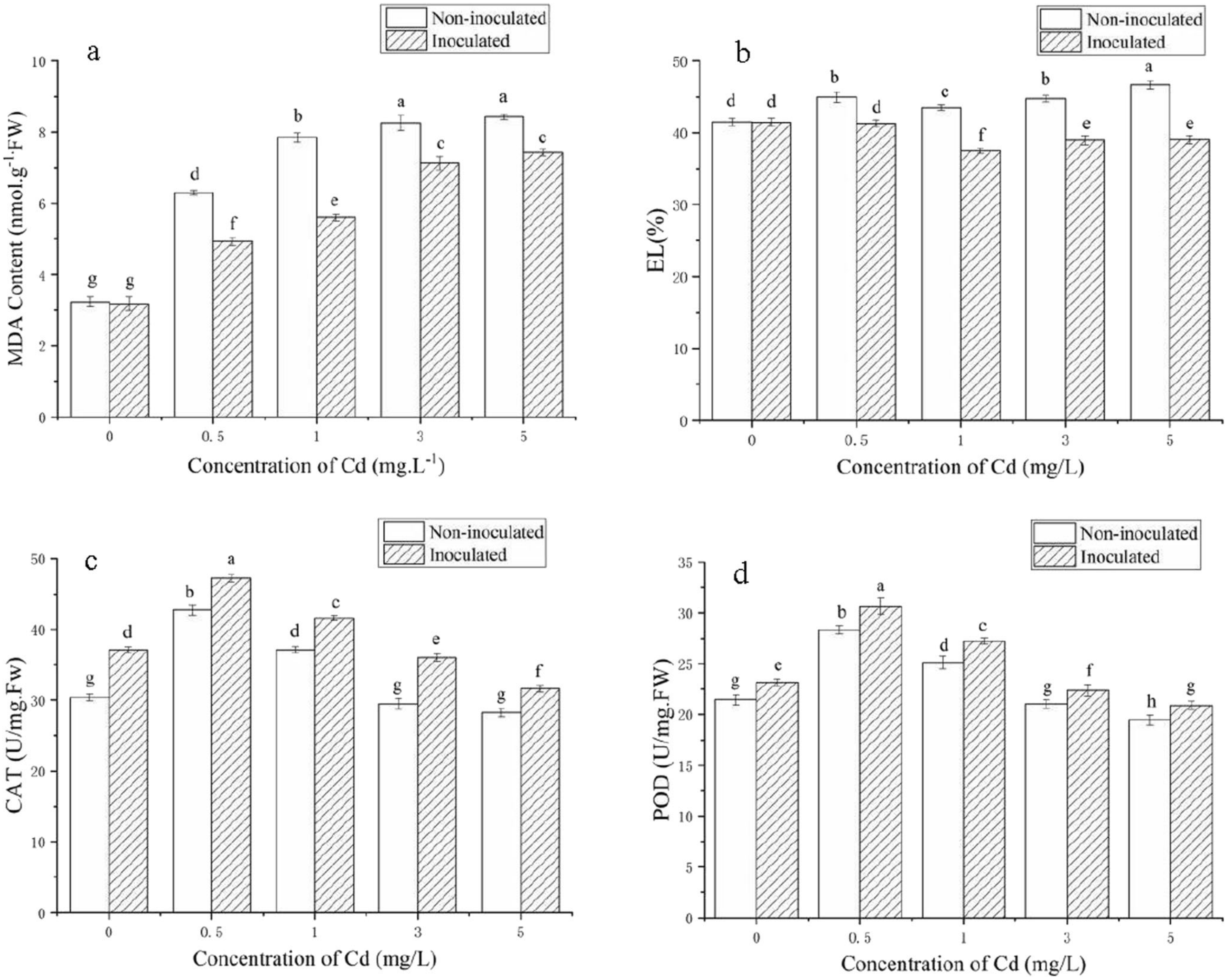


Fig. 5 Effect of Zm-123 inoculation on MDA level (a), EL level (b), CAT activity (c), and POD activity (d) in edible parts of rape seedlings at different Cd concentrations after 4 weeks

Accumulation of Cd in rape seedlings

Apparently, Cd concentrations in edible parts of rape seedlings inoculated with Zm-123 were significantly lower ($p < 0.05$) as compared with those in non-inoculated (Fig. 6(d)). In addition, under different concentrations of Cd, the Cd contents ranged from 0.25 to 0.85 mg/g in the non-inoculated group and from 0.16 to 0.75 mg/g in the inoculated group. Inoculation decreased Cd contents by 35.87%, 19.38%, 18.57%, and 11.13% compared with those in the non-inoculated group at Cd concentrations of 0.5, 1, 3, and 5 mg/L, respectively. Particularly, Zm-123 inoculation had the best effect on Cd reduction at 0.5 mg/L of Cd.

Discussion

Several *Enterobacter* spp. have been reported to possess high Cd resistance and PGP properties that can be potentially used in microbe-assisted phytostabilization (Abd El-Azeem et al. 2012; Pramanik et al. 2018; Madhaiyan et al. 2010). In the present research, a novel *Enterobacter* sp. Zm-123 with multiple metal resistance and PGP traits including IAA production, siderophore production, and phosphate solubilization activity was isolated. Our study clearly indicated that strain Zm-123 tolerated the maximum limit of Cd^{2+} ions up to 600 mg/L, which was much higher than previously isolated *Enterobacter* sp. MH8b (225 mg/L) (Płociniczak et al. 2013) and *Enterobacter* sp. CIK-521 (325 mg/L) (Ahmad et al. 2016). Moreover, it possesses much higher capability in IAA production, siderophore production, and phosphate solubilization activity than other *Enterobacter* spp. (Liu et al. 2018; Singh et al. 2018). Many studies indicated that the actual PGP effects might be quite different in the interactions between different plants, bacteria, and metals, which would greatly influence the final remediation efficiency of microbe-associated phytostabilization. Therefore, this study devoted to

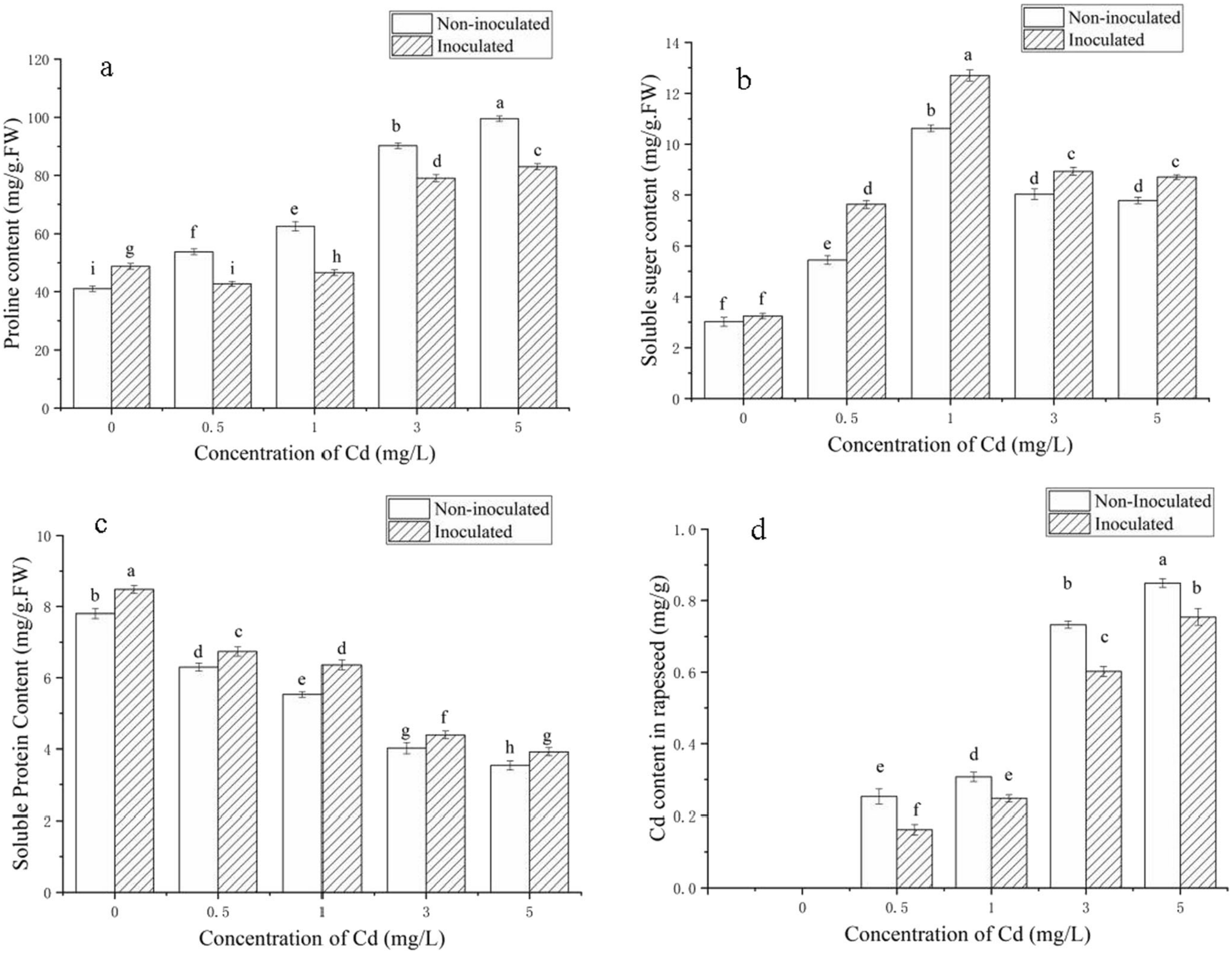


Fig. 6 Effect of Zm-123 inoculation on proline content (a), soluble sugar content (b), soluble protein content (c), and Cd uptake (d) in edible parts of rape seedlings at different Cd concentrations after 4 weeks

investigating the actual effect and potential mechanism of Zm-123 on the growth of rape seedlings under Cd stress.

Effects of IAA production on physiological characteristics and antioxidant capacity of rape seedlings

Cd has an adverse impact on plant growth by interfering with the physiological process and decreasing the antioxidant capacity (Dell'Amico et al. 2008). Indole-3-acetic acid (IAA) is the most abundant and naturally occurring auxin, well known for its regulatory function in plant growth and stress resistance (Fässler et al. 2010). Agami and Mohamed (2013) reported that exogenous IAA has significantly increased root and shoot length, photosynthetic pigment content, many physiological parameters, and antioxidant enzyme activities in wheat (*Triticum aestivum* L.). Exogenous IAA also greatly increases the contents of soluble sugar and protein in plants under Cd stress (Zhang et al. 2020) and protects plants from Cd-induced oxidative damage by rapidly degrading MDA and proline accumulated in various parts of plants (Ran et al. 2020). In the present study, Zm-123 was also found to enhance root elongation regardless of the presence of Cd and increased the chlorophyll content by 96.67% at Cd concentration of 5 mg/L. In addition, application of Zm-123 increased soluble sugar and soluble protein in rape seedlings by 40.00% and 7.00% and by 11.96% and 10.73% at 0.5 mg/L and 5 mg/L Cd, respectively. Furthermore, Zm-123 significantly decreased MDA by 28.66% and proline by 25.57%, and increased CAT and POD in leaves by 12.12% and 8.44% at 1 mg/L Cd compared with that in non-inoculated treatment, respectively. In agreement with our results, a similar reduction rate in MDA and proline content was found in the *Brassica juncea* seedlings inoculated by *Enterobacter* sp. IU02 exposed to Cd (Ullaha et al. 2019), while a promotion in CAT and POD activity was found in the research of rice seedlings inoculated with *Enterobacter* sp. K6 under Cd stress (Pramanik et al. 2018). Combined with these results, it can be deduced that

Zm-123 inoculation can significantly improve the physiological characteristics and antioxidant capacity of rape seedlings under Cd stress.

Effects of phosphate solubilization on plant growth, antioxidant capacity, and Cd uptake in rape seedlings

Phosphorus (P) as an essential macro-element is involved not only in plant growth and cell function (Dai et al. 2017) but also in the absorption and transportation of Cd (Dai et al. 2018). High concentrations of heavy metals in the rhizosphere inhibit the transportation of phosphate and other essential nutrients, while plant-associated bacteria can replenish these nutrients through solubilizing phosphate and reducing Cd uptake in the root (Jia et al. 2020). Previous reports showed that inoculation of the phosphate-solubilizing *Serratia* sp. significantly enhanced plant growth parameters including chlorophyll contents, root and shoot lengths, and biomass (Yu and Zhou 2009). Zm-123 can solubilize 13.58 to 137.5 mg/L of phosphate at different concentrations of Cd, which may help rape seedlings to acquire more P nutrients and increase the fresh weight, root length, and chlorophyll contents subsequently. P supply also can promote the antioxidant system and reduce lipid peroxidation in plants under Cd stress by increasing the related gene expression (Wang et al. 2015). In the present study, MDA content and antioxidant enzyme activities were greatly reduced by the inoculation of Zm-123, which might be attributed to phosphate solubilized by Zm-123. In addition, the previous experiment also demonstrated that P supplementation increased Cd accumulation in the roots in mangrove seedlings subjected to Cd stress, indicating that much of Cd was fixed in the root, rather than transported to shoot (Dai et al. 2017). In the present study, Cd contents in edible parts of rape seedlings also decreased after application of Zm-123 compared with those in non-inoculated treatment.

Effects of siderophore production on plant growth and Cd content in rape seedlings

Cd can impede plants to assimilate essential elements, such as Mn and Fe, which inhibit chlorophyll synthesis, disturb the chloroplast ultrastructure, or cause chlorophyll degradation (Sinha and Mukherjee 2008). Siderophores as iron-chelating agents are generally produced by microorganisms under iron-limiting conditions or metal stress (Braud et al. 2009). PGPB with siderophores producing capability can supply unavailable form of Fe^{3+} to the plant and accelerate its mobility in the rhizosphere (Rajkumar et al. 2012). Inoculation of Zm-123 increased the chlorophyll contents in rape seedlings under Cd stress. Similar to our study, Dimkpa et al. (2009) reported that there was an increase in chlorophyll content after application of the siderophore-producing bacterium. Moreover, it has been reported that microbial siderophores have potential in metal uptake and mobilization or metal resistance development in the presence of toxic metals (Gaonkar and Bhosle 2013). Kumari et al. (2019) have found that siderophores from *Aspergillus nidulans* significantly recovered the plant growth and declined As accumulation in wheat by elevating the SOD, CAT, and POD activities under As stress. Siderophores originated from PGPB might also increase Fe acquisition and decrease Cd uptake in plants by inhibiting the expression of iron-regulated transporter (IRT) (Fan et al. 2014; He et al. 2017; Luo et al. 2012). Upon Zm-123 treatment, Cd accumulation in edible parts of rape seedlings was decreased considerably, supporting our view that siderophore could bind with the metal ions and interfere with their entry into the plants.

Conclusion

In conclusion, the isolated strain *Enterobacter* sp. Zm-123 is a Cd-resistant bacterium with PGR characteristics including IAA and siderophore production and phosphate solubilization ability. Inoculation of Zm-123 can improve root elongation and physiological status, alleviate oxidative stress, and reduce Cd uptake in rape seedlings under Cd. The newly isolated *Enterobacter* sp. Zm-123 may be a suitable candidate for microbe-assisted phytostabilization due to its high Cd resistance and PGP properties.

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