Cadmium resistance, microbial biosorptive performance and mechanisms of a novel biocontrol bacterium *Paenibacillus* sp. LYX-1

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Received: 25 October 2021 / Accepted: 29 April 2022 / Published online: 11 May 2022
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Abstract

In this study, a novel biocontrol bacterium was isolated and identified as *Paenibacillus* sp. LYX-1 from soils in the peach orchard. Both Cd\(^{2+}\) resistance and biosorption behavior of strain LYX-1 was explored. Meanwhile, the Cd\(^{2+}\) resistance and biosorption mechanisms were further identified by Cd-resistant genes, SEM–EDS, FTIR, XPS, and TEM analysis. The results showed that strain LYX-1 could resist 50 mg/L Cd\(^{2+}\) and had the CzcD gene responsible for Cd\(^{2+}\) efflux. Under pH 8.0 and at a dose of 1.0 g/L sorbent dose, the removal efficiencies of living and dead cells were as high as 90.39% and 75.67% at 20 mg/L Cd\(^{2+}\), respectively. For the adsorption isotherm test, results revealed that both Langmuir (\(R^2 = 0.9704\)) and Freundlich (\(R^2 = 0.9915\)) model could describe the Cd\(^{2+}\) biosorption well for living strain LYX-1. The maximum equilibrium biosorption capacities of living and dead biomass were 30.6790 and 24.3752 mg/g, respectively. In the adsorption kinetic test, the adsorption process of both living and dead strain LYX-1 all satisfied the pseudo-second kinetic equation. A desorption study showed that strain LYX-1 sorbents could be recycled and regenerated by eluents efficiently. SEM–EDS analysis reflected that Cd\(^{2+}\) was bound to the cell wall. Besides, the biosorption process was controlled by chemisorption with the participation of the -OH, -NH, -C=O, O=C-O, C-N, S\(^2^-\), and phosphate functional groups on the cell surface of strain LYX-1, which were identified by FTIR and XPS. Bioaccumulation also made a contribution to the Cd\(^{2+}\) removal during the biosorption process of living sorbent. The above results indicated that strain LYX-1 had higher Cd\(^{2+}\) tolerance and Cd\(^{2+}\) removal capacity. This strain exhibits promising application to the removal of Cd\(^{2+}\) in the Cd-contaminated environment.

Keywords *Paenibacillus* sp. · Biocontrol · Cd · Resistance · Biosorption · Mechanisms

Introduction

Heavy metals (HMs) are the main pollutants in the development of mineral resources, textile, fertilizer manufacturing, metal smelting, and processing (Jin et al. 2019). Cadmium (Cd) designated as one of the priority pollutants controlled by many countries can participate in the food chain cycle, accumulate in the organism, and eventually cause irreversible tubular damage in the kidney after it enters the environment (Jin et al. 2020). Therefore, effective treatment of heavy metal Cd pollution in soil and water has become an important issue that needs to be solved urgently in the field of environmental protection today.

Compared with conventional chemical precipitation, electrolysis, reverse osmosis, ion exchange, etc., microbial adsorption had significant advantages, mainly including high efficiency, abundant raw materials, coupled with high chemical activity (Li et al. 2018; Shi et al. 2021; Sun et al.)
Additionally, in domestic and international pieces of literature, more and more strains employed as environmentally friendly biomasses have been applied in the removal of metal ions, such as Comamonas sp. XL8 (Shi et al. 2021), Enterobacter sp. DNB-S2 (Sun et al. 2020), Serratia liquefaciens CL-1, and Bacillus thuringiensis X3 (Han et al. 2018). Besides, numerous pieces of evidence have proved that biological cell components (e.g., cell wall polysaccharides, proteins, lipid molecules) realized the removal of heavy metals through chelation, ion exchange, biosorption, inorganic micro-precipitation, redox, and diffusion (Badescu et al. 2018; Huang et al. 2014; Özdemir et al. 2009; Tan et al. 2020; Zhou et al. 2018). At present, the environment polluted by HMs is widespread, and there are few reports on the adaptability of the currently used biocontrol bacterium as microbial materials for heavy metal pollution control under the stress of HMs. The search and discovery of biocontrol bacterium that have high tolerance and immobilization to HMs are of great significance to the restoration and utilization of the heavy metal-contaminated environment.

Paenibacillus sp. is a kind of significant disease biological control microorganism, which due to its ability to produce a variety of enzymes for degrading the cell wall, e.g., chitinases, cellulases, proteases, and β-1,3-glucanases (Hao et al. 2017). In the previous study, Paenibacillus sp. showed diverse antagonistic activities against five phytopathogenic fungi (Fusarium graminearum, Magnaporthe oryzae, Rhizoctonia solani, Sclerotinia sclerotiorum, and Botrytis cinerea) (Ali et al. 2020). Researches over the past decades showed that Paenibacillus sp. could produce a variety of antibiotics, polymyxin, hydrolases, and other antagonistic substances (Ali et al. 2020; Araujo et al. 2020), which was one of the important mechanisms for the biocontrol of Paenibacillus sp. (Hao et al. 2017). Paenibacillus sp. can not only offer protection against bacteria, fungi, nematodes, and viruses, but also has advantages of non-pathogenicity, non-toxicity, good environmental compatibility, less residue, safety for humans and animals. Nevertheless, the survival of biocontrol bacterium employed for prevention and control of plant diseases is prone to be threatened by toxic Cd, pests, and diseases in composite pollutant sites (Olaniran et al. 2013). Therefore, finding a Paenibacillus sp. with high tolerance and removal capacity for Cd is of great significance for the simultaneous control of soil Cd pollution and plant rhizosphere disease. However, relevant studies are rarely reported.

In the present work, a novel biocontrol strain Paenibacillus sp. LYX-1 having antagonistic to peach brown rot and higher Cd resistance was isolated from soil in the peach orchard. The Cd resistance, microbial biosorptive performance, and mechanisms of Paenibacillus sp. LYX-1 were studied, including (1) investigate the Cd resistance and mechanisms of biocontrol Paenibacillus sp. LYX-1, (2) compare the biosorption process of living and dead biosorbents, closer to the real-world scenarios where nutrients are deficient, (3) describe the biosorption performance of the living and dead cells via kinetic and isotherm models, (4) study the desorption efficiency of both living and dead biosorbents, and (5) explore the Cd$^{2+}$ biosorption mechanisms through SEM-EDS, FTIR, XPS, and TEM analysis. The main aim of such work was to develop and provide a novel microbial biosorbent with a high capacity to adsorb Cd$^{2+}$, which can be used to remediate Cd$^{2+}$-contaminated environment.

**Materials and methods**

**Isolation and identification of biocontrol strain**

Biocontrol strain was isolated in the following steps. Ten grams of rhizosphere soil in a peach orchard in Fenghua city, Zhejiang province, China (29°39′40.99″N, 121°16′40.06″E) was initially suspended in 90 mL of sterile water and incubated at 180 rpm, 30 °C for 1 h. The gradient dilution method was used to dilute the soil into soil suspensions with sterile water. 0.1 mL 10$^{-4}$, 10$^{-5}$, and 10$^{-6}$ gradient dilutions were applied to Luria–Bertani’s (LB) agar plate consisted of 10.0 g/L tryptone, 5.0 g/L yeast extract, 10.0 g/L NaCl, and 20.0 g/L agar. Three replicates for each gradient were incubated at 30 °C for 48 h. (1) Primer screening: 6-mm diameter peach brown rot fungus taken by a hole puncher was placed in the center of the PDA plate. And then, the strains to be screened were placed on 4 corners 3 cm away from the center of the plate and incubated at 28 °C for 48 h. Twenty-four strains that shrunk the peach brown rot fungus were selected and saved as re-screening objects. (2) Fine screening: the peach brown rot fungus and re-screening strains were inoculated on PDA plates through a 6-mm hole punch again, respectively. Above plates were also incubated at 28 °C for 48 h to observe the size of the inhibition zone. And, the PDA plate inoculated with only peach brown rot fungus was set as a control to measure the diameter of the inhibition zone. Finally, the strain with maximum inhibitory diameter was retained as the target strain that has the highest antagonistic on peach brown rot fungus for further research.

The 16S rDNA extracted from the strain with the highest antagonistic effect on peach brown rot, as a PCR template, was amplified and sequenced using the universal primers 27F (5′-AGTTTGTACMTGGCTCAG-3′) and 1492R (5′-GTTACCTTGTAGACTT-3′) according to previous study (Galkiewicz and Kellogg 2008). The nucleotide sequence was compared in the GenBank database (Nucleotide Blast) using the BLAST search tool to accurately identify the bacterium (Tan et al. 2020). Meanwhile, the neighbor-joining method was selected to construct sequencing
results of biocontrol strain into a phylogenetic tree through MEGA 7.0 software.

**Cd²⁺ resistance of the biocontrol strain LYX-1**

**Cell growth curves under Cd²⁺ stress**

The pure cultured strain LYX-1 at logarithmic growth phase ($OD_{600} = 1.5 ± 0.2$) were seeded in LB medium containing different Cd²⁺ concentrations (0, 5, 10, 20, 50, 100 mg/L) at 2% inoculation amount; meanwhile, conical flasks were incubated for 62 h at 30 °C with 150 rpm on a shaker. The OD₆₀₀ values were monitored at different time intervals using an ultraviolet spectrophotometer (Shimadzu UV-2450, Japan) to construct growth curves. The Cd ion stock solution used in the above experiment was prepared in a 1000-mL volumetric flask by dissolving 2.74 g Cd(NO₃)₂·4H₂O (analytical grade) purchased from Sinopharm Chemical Reagent Co., Ltd. (Shanghai, PRC) in deionized water (Millipore, 18.2 MΩ cm).

**PCR amplification of Cd²⁺-resistant genes**

According to the current research about the mechanism of strain resistance to Cd²⁺, its resistance was mainly controlled by universal cadA and Czc systems (Ayangbenro et al. 2019; NIES et al. 1998; Wei et al. 2009). The resistance genes of strain LYX-1 were screened and predicted through PCR amplification of related Cd-resistance genes in microorganisms (cadA, CzcA, CzcB, and CzcD). The genomic DNA of strain LYX-1, used as a PCR amplification template, was amplified as follows: pre-denaturation at 98 °C for 3 min; 35 cycles of denaturation at 98 °C for 10 s, annealing at X °C for 10 s, extension at 72 °C for 15 s; followed by a final extension step at 72 °C for 3 min. The primer sequences selected with reference to the previous studies of the above-mentioned enzyme genes were listed in Table S1. All primers used for PCR were synthesized by Tsingke Biotechnology Co., Ltd. (Beijing, China).

**Sorbent preparation**

The pure cultured strain LYX-1 was seeded in 600-mL sterile LB medium in 1000-mL flasks at 1% inoculation amount and cultured for 48 h at 30 °C, 150 rpm at a constant temperature shaker. Living cell adsorbent was prepared by centrifuging the bacterium suspension at 4 °C, 8000 rpm for 10 min, while dead cell adsorbent was harvested by centrifuging the bacterial suspension that has been sterilized at 121 °C for 30 min. Both living and dead pellet were washed 3 times and resuspended with sterile water; then, biomass was stored in a 4 °C refrigerator until use. The concentration (grams per liter) of the above cell suspension was tested by drying an aliquot to constant weight at 80 °C (Huang et al. 2013).

**Biosorption Cd²⁺ experiments by strain LYX-1**

**pH effects**

The initial solution pH values from 3 to 8 for the sorption experiment were adjusted using 1.0 M NaOH and 1.0 M HNO₃. Sorption experiments were conducted in 50-mL centrifuge tubes containing 20 mL Cd²⁺ aqueous solution, 1.0 g/L living, and dead sorbents, which were agitated at a speed of 180 rpm for 6 h. The metal solutions used for the sorption experiments were diluted from 1000 mg/L (metal concentration) Cd(NO₃)₂ stock solution. All experiments were performed at ambient conditions and in triplicate. The sorbents were removed by centrifugation at 10,000 rpm for 10 min and the supernatant filtrated through a 0.22-μm filter (PVDF, Sterile) was used to measure the remaining Cd²⁺ via ICP-MS (Perkin Elmer 600X, USA). The pH was measured by a pH meter (PHS-25, INESA, China).

**Biosorbent dosage effects**

To examine the effects of the biosorbent dosage, the biosorption experiments were carried out at different dosages (0.2–3.0 g/L). The experiments were performed at optimal pH 8, 30 °C, 180 rpm, and 50 mg/L Cd²⁺ for 6 h. All experiments were performed at ambient conditions and in triplicate.

**Contact time effects and sorption kinetic characteristics**

The optimal pH (8.0) and biomass (1.0 g/L) was mixed with different contact time (0–300 min) at 50 mg/L Cd²⁺. All experiments were performed at 30 °C, 180 rpm for 6 h, and in triplicate. To determine the rate-limiting steps of Cd²⁺ biosorption by strain LYX-1, pseudo-first- and pseudo-second-order rate models were used to fit the kinetic experimental data to study the biosorption mechanism.

Pseudo-first-order kinetic model has long been widely applied (Ho 2006), the form is:

\[ \ln(q_e - q_t) = \ln(q_e) - k_1 t \]  

where $q_e$ and $q_t$ are the amounts of the Cd²⁺ sorbed at equilibrium and at any time $t$ (mg/g) and $k_1$ is the pseudo-first-order rate constant of sorption (1/min).

The pseudo-second-order kinetic equation (Ho and McKay 1999) is shown below:

\[ \frac{t}{q_t} = \frac{1}{K_2q_e^2} + \frac{t}{q_e} \]  

where $q_e$ and $q_t$ are the amounts of the Cd²⁺ sorbed at equilibrium and at any time $t$ (mg/g) and $k_1$ is the pseudo-first-order rate constant of sorption (1/min).
where \( k_2 \) is the pseudo-second-order rate constant, g/(mg min), respectively, and \( q_e \) and \( q_l \) (mg/g) were defined elsewhere.

**Initial Cd\(^{2+}\) concentrations and sorption isotherm experiments**

The optimal pH (8.0) and biomass (1.0 g/L) was mixed with different concentrations of Cd\(^{2+}\) (0–50 mg/L). All experiments were performed at 30 °C and 180 rpm in triplicate. The Cd biosorptive performance of the strain LYX-1 was simulated by using Langmuir and Freundlich isotherm equations, as follows (Freundlich 1906; Langmuir 1918):

\[
\text{Langmuir equation: } q_e = \frac{q_{\text{max}} k_L C_e}{1 + K_L C_e} 
\]

\[
\text{Freundlich equation: } q_e = K_f C_e^{1/n} 
\]

where \( q_e \) is the amount of Cd sorbed at equilibrium (mg/g), \( C_e \) is the Cd equilibrium concentration (mg/L), \( q_{\text{max}} \) is the saturated sorption capacity of an aqueous solution for Cd\(^{2+}\), and \( K_L \) is a Langmuir constant related to the sorption strength. Here, \( K_f \) is the Freundlich coefficient indicating sorption capacity, \( n \), a constant related to Cd ion concentration, characterizes adsorption intensity, respectively, and \( q_e \) and \( C_e \) were described earlier.

Another dimensionless constant separation factor \( R_L \) of the Langmuir isotherm model can be expressed as follows:

\[
R_L = \frac{1}{1 + K_L C_0} 
\]

where \( C_0 \) is the highest Cd\(^{2+}\) concentration (mg/L), \( K_L \) is a Langmuir constant, \( R_L \) reflects the nature of biosorption process (\( R_L > 1 \): unfavorable; \( R_L = 1 \): linear; \( 0 < R_L < 1 \): favorable; \( R_L = 0 \): irreversible).

The Dubinin-Radushkevich (D-R) was selected to study the nature of the sorption phenomena either physical or chemical sorption, governing the characteristic of not assuming a homogeneous surface or constant adsorption potential (Dubey and Gupta 2005; Zhou et al. 2018). It can be expressed as:

\[
\ln q_e = \ln q_{\text{max}} - \beta \varepsilon^2 
\]

where \( q_e \) (mg/g) and \( q_{\text{max}} \) (mg/g) are described above, \( \beta \) (mol\(^2\)/kJ\(^2\)) is the parameter with respect to the mean free energy of sorption per molecule of the adsorbate, \( \varepsilon \) (kJ/mol) is the adsorption potential, and the mean free energy \( E \) (kJ/mol) can be computed using following formula (Kaur et al. 2015):

\[
E = \frac{1}{2\beta} 
\]

For the adsorption from the aqueous solution, the adsorption potential can be defined as (Hu and Zhang 2019):

\[
\varepsilon = RT \ln \left(1 + 1/C_e\right) 
\]

**Desorption experiments**

The first step in these experiments was to perform duplicate sets of biosorption experiments. Both 1.0 g/L living and dead sorbents were soaked into 50-mL centrifuge tubes containing 20 mL 50 mg/L Cd\(^{2+}\) aqueous solution, respectively, which were performed at 30 °C and 180 rpm for 6 h. The sorbents were gathered by centrifugation at 10,000 rpm for 10 min and the supernatant filtrated through a 0.22-μm filter (PVDF, Sterile) was to measure the remaining Cd\(^{2+}\) via ICP-MS. Meanwhile, the Cd-laden living and dead sorbents were washed using deionized water three times. Then, two sorbents were resuspended in eluents (0.1 M HNO\(_3\) and 0.1 M Na\(_2\)EDTA) with equivalent volumes, respectively (Soh et al. 2022; Zhou et al. 2014). Finally, the desorption experiments were carried out at 30 °C and 180 rpm for 3 h. And, the desorbed Cd\(^{2+}\) in the supernatant was measured through ICP-MS.

\[
\text{Desorption efficiency(%) } = \frac{C_{\text{des}}}{C_e} \times 100 
\]

where \( C_{\text{des}} \) (mg/L) is the amount of Cd ion concentration in desorbing agent after the desorption step and \( C_e \) (mg/L) is the Cd equilibrium concentration in the supernatant after the biosorption step.

**Characterization of biosorption mechanisms of Cd\(^{2+}\) by strain LYX-1**

Samples of living and dead cells before and after 50 mg/L Cd\(^{2+}\) biosorption were collected and freeze-dried for the following tests. Cells were immobilized in glutaraldehyde at 4 °C overnight and then washed using phosphate buffer (pH 7.2) for 3 times. The washed biomass was finally dehydrated in alcohol and followed by immobilization and being cut into 70–90-nm shin sheets for transmission electron microscopy (H-7650, Japan), scanning electron microscope coupled with energy dispersive spectroscopy (Nova Nano 450, USA) analysis. Freeze-dried biomass was prepared for Fourier transform infrared spectroscopy (Thermo Scientific Nicolet iN10, USA) and X-ray photo-electron spectroscopy (Thermo Scientific K-Alpha, USA) to study the fundamental properties and underlying encapsulation mechanisms of...
adsorbents before and after biosorption according to previous methods (Huang et al. 2020).

**Statistical analysis**

All experiments were performed in triplicates. Statistical analysis was carried out using SPSS 20.0 software. All drawings and model fittings were generated using Origin 2018 software. The phylogenetic tree was constructed by MEGA 7.0.

**Results and discussion**

**The isolation and identification of biocontrol strain* Paenibacillus* sp. LYX-1**

Biocontrol strain* Paenibacillus* sp. LYX-1 with antagonistic to peach brown rot was isolated from rhizosphere soil in a peach orchard in Fenghua city, Zhejiang province, China. The significant antagonism to peach brown rot could be seen in the plate antagonism test from Fig. S1. The 16S rDNA sequences of LYX-1 aligned with the published sequences in the NCBI database using BLAST (https://www.ncbi.nlm.nih.gov) had the highest similarity (99.62%) with* Paenibacillus* sp. The phylogenetic tree constructed also indicated that the strain had a 99% threshold with* Paenibacillus* sp. (Fig. 1a). Thus, it was named* Paenibacillus* sp. LYX-1 and its GenBank accession number was MZ234160. Strain LYX-1 has also been deposited in China General Microbiological Culture Collection Center (CGMCC accession No. 22158) as a patent strain. The strain on LB medium was round, light yellow with smooth edges (Fig. 1b). Figure 1c proved that strain LYX-1 was Gram positive.

**Cd²⁺ resistance and mechanism of* Paenibacillus* sp. LYX-1**

**Effects of Cd²⁺ concentrations on growth curves of strain LYX-1**

Microbial growth was influenced directly by the microbial activity under different concentrations of heavy metals (Huang et al. 2014; Sun et al. 2020; Tan et al. 2020). As shown in Fig. 2, the growth of* Paenibacillus* sp. LYX-1 was barely affected and the maximum OD₆₀₀ value even exceeded 2.4 under 20 mg/L Cd²⁺. As the concentration
Increased, the logarithmic growth stage had obvious delays, which might due to stressed metabolic pathway and internal biochemical reactions (Sun et al. 2020). Increasing the Cd2+ concentrations did not significantly decrease the strain LYX-1 activity (Fig. 2), suggesting that the stain LYX-1 had a good environmental adaptability that could continue to grow in the presence of 50 mg/L Cd2+. However, strain LYX-1 did not grow when Cd2+ in solution reached 100 mg/L. In sum, the strain LYX-1 had relatively high Cd2+ resistance (50 mg/L), probably because strain LYX-1 could mobilize internal mechanisms such as surface biosorption and intracellular accumulation to remove Cd2+ in solutions to alleviate the toxicity of Cd2+ for cells (Sun et al. 2020).

Similar to other bacteria, strain LYX-1 might secrete extracellular polymers including polysaccharides, proteins to complex, chelate, and precipitate Cd2+ to reduce the toxicity of Cd2+ in solution during the growth process (Xie et al. 2020). Besides, it is necessary and helpful to determine the Cd resistance molecular mechanisms of strain LYX-1.

Amplification of Cd2+‑resistant genes of strain LYX-1

Paenibacillus sp. LYX-1 resistant to Cd2+ was chosen for sequence analysis of the cadA, CzcA, CzcB, and CzcD, which had the potential to reduce or eliminate heavy metal Cd2+ toxicity (Wei et al. 2009). Fig. S2 showed that Paenibacillus sp. LYX-1 processed Cd2+‑resistant genes (CzcD) that could modify the protein, determine the specificity to the metal substrate, and realize the resistance to Cd through the efflux system (Legatzki et al. 2003). To a certain, the determination of the CzcD gene of Paenibacillus sp. LYX-1 indicated that strain LYX-1 could effectively mobilize the molecular mechanism to alleviate the toxicity of Cd2+ through its efflux system (Legatzki et al. 2003). It also further explained the phenomenon that strain LYX-1 could tolerate high concentrations of Cd2+ (50 mg/L). Furthermore, the nucleotide sequence of the Cd-resistant gene in Paenibacillus sp. LYX-1 was translated into a protein sequence and aligned with protein partial sequences of other Cd-resistant bacteria through MEGA 7.0 software. The phylogenetic tree based on the CzcD protein partial sequence was constructed by the neighbour-joining method (Fig. S3). Cd-resistant PCR fragment in strain LYX-1 showed a high homology with cadmium resistance protein CzcD from Caulobacter vibrioides NA1000 (Genomic Sequence: YP_002515680.1).

Impact factors optimization to Cd2+ adsorption by Paenibacillus sp. LYX-1

The Cd2+ biosorption performance of the living and dead biomass was complex, and the removal efficiency of Cd2+ was closely related to pH, initial Cd2+ concentrations, doses, and contact time (Yu and Fein 2017; Zhou et al. 2014). To investigate the sorption conditions of living and dead sorbents, the effects of these four independent variables were illustrated.

Effects of different pH

Most of the studies have shown that pH was an important factor affecting the biosorption process, because it could directly influence the solubility of metal ions, ionization state of functional groups on the microorganism surface (Altowayti et al. 2019; Şahin and Öztürk 2005). As the initial pH increased, Cd2+ removal showed a rising tendency (Fig. 3a). Due to the competitive adsorption between hydrogen ions and adsorbed Cd2+ ions (Zeng et al. 2021), the equilibrium adsorption capacity of heavy metal was just 7.95 mg/g and 6.48 mg/g for living and dead cells at the pH 3.0. When the pH reached 4.0, more charged functional groups on the cell surface, such as carboxyl, amino, and hydroxyl began to expose, which strengthened the binding of Cd2+ to the adsorption site, thereby increasing the amount of adsorption (Li et al. 2018; Özdemir et al. 2009). Meanwhile, as the solution pH increased, more Cd2+ would be fixed onto the negatively charged cell surface due to the electrostatic adsorption. Notably, in the presence of a highest point between pH 3 and 8, the optimum pH value for sorption was determined at 8.0 for both living cells and dead cells, which suggested that the LYX-1 had an excellent pH buffering performance (Moussous et al. 2012; Wang and Chen 2014; Yaashikaa et al. 2021). It was calculated that when pH = 8.0, heavy metal ions not reach the precipitation equilibrium constant, so hydroxide precipitation was not generated in the solution.
Effects of initial Cd²⁺ concentrations

Figure 3b showed the adsorption capacity of Paenibacillus sp. LYX-1 at different Cd²⁺ concentrations ranging from 0 to 50 mg/L. In general, with the increase of the initial concentrations of Cd ions, the biosorption capacity gradually increased for both living and dead cells, which implied that an increase in the initial Cd²⁺ concentration generated a diving force and reduced the mass transfer resistance between Cd ions and sorbents (Masoudzadeh et al. 2011). Owing to the limited biosorption sites of sorbents, the sorption capacity reached saturation in higher concentration treatment (more than 30 mg/L). In addition to the adsorption of living cells, there was also intracellular accumulation (Li et al. 2010). Herein, the adsorption capacity of living cells (18.019 mg/g) was slightly higher than dead cells (14.847 mg/g) when Cd²⁺ concentration was 20 mg/L. Note that the removal capacities of living and dead cells were as high as 90.39% and 75.67% under the 20 mg/L Cd²⁺, respectively. Thus, Paenibacillus sp. LYX-1, as an environmentally friendly and cheap biosorbent resource, could be applied for the treatment of the Cd-contaminated environment.

Effects of adsorbent dose

The variation of equilibrium uptake for Cd ions at different biosorbent doses for each living biomass and dead biomass was shown in Fig. 3c, which indicated that Cd²⁺ was adsorbed by the living biomass more strongly than dead biomass and two adsorbents had similar patterns for Cd removal. The adsorption capacity increased gradually as the biomass dose increased from 0.2 to 1.0 g/L, which could be explained that more binding sites were available, and thus, the biosorption capacity went up with the increase in dose (Sun et al. 2011). However, the biomass of strain LYX-1 presented a declining trend with an increased biosorbent dose from 1.0 to 3.0 g/L. It has been reported that biosorbent generated aggregation under high biosorbent concentrations, causing a decrease in the effective contact area between cells and metal ions (Zhu et al. 2016).
Therefore, the optimum living and dead cell dosage of all following experiments was selected as 1.0 g/L. Therefore, it was obvious that redundant adsorbents were not necessary for an efficient biosorption performance under a specific initial concentration.

**Effects of contact time**

As reported by Sun et al. (2011), contact time had a significant effect on the equilibrium biosorption. Cd\textsuperscript{2+} biosorption by *Paenibacillus* sp. LYX-1 under different contact time (0–300 min) at 50 mg/L initial Cd\textsuperscript{2+}, pH 8.0, 30 °C, and 180 rpm was studied. The effect of contact time on the amount biosorbed was presented in Fig. 3d. For Cd\textsuperscript{2+}, saturation levels of living and dead biomass were obtained after 120 min and 60 min, respectively, which indicated that LYX-1 had a higher adsorption efficiency. The biosorption capacity of the two adsorbents for Cd increased with the extension of time. It showed a fast adsorption process within 30 min and a slow adsorption process within 30–60 min for a dead biosorbent. This was because the adsorption sites on the bacterial surface gradually reached saturation. After reaching 60 and 120 min, the adsorption curve showed a relatively gentle trend, indicating that the adsorbent and adsorbate reached adsorption equilibrium. The shaking time was determined to be 3 h for the rest of the batch experiments to make sure the equilibrium was reached.

**Adsorption kinetic characteristics**

In this study, pseudo-first- and pseudo-second-order kinetic models were selected to describe the dynamic performance of strain LYX-1 for Cd\textsuperscript{2+}. According to Eqs. (1) and (2), the experimental data was fitted to obtain the kinetic fitting diagrams (Fig. 4a and b). As shown in Table 1, the values of the corresponding correlation coefficient $R^2$ obtained using the pseudo-second-order model for living and dead biomasses were 0.9894 and 0.9798, respectively. These values of $R^2$ were greater than the values of 0.7273 and 0.7365 for living and dead cells, respectively, obtained using the pseudo-first-order model (Table 1). The above results reflected that the effect of the pseudo-second-order rate equation was better than the pseudo-first-order rate equation, further indicating that the influence of the mass diffusion step on the adsorption rate could be negligible and the rate-limiting step was a chemical adsorption process (Ho 2006; Ho and McKay 1999). This result was consistent with numerous reports about the kinetic adsorption process of microbial biosorbents for heavy metals (Abdolali et al. 2016; Feng et al. 2011. Besides, the reaction rate $k$ value of dead cells was higher than living cells, indicating that the biosorption rate for Cd\textsuperscript{2+} of dead sorbent was faster than living sorbent (Table 1). Furthermore, the calculated equilibrium adsorption capacity of Cd\textsuperscript{2+} using a pseudo-second-order equation was consistent with the measured values for two biosorbents (Table 1). However, the values of the calculated $q_e$ by the
pseudo-first-order Eq. (7.7250 mg/g and 5.7030 mg/g for living and dead sorbents, respectively) differed greatly from the values of measured \( q_e \) (23.7158 mg/g and 20.5453 mg/g for living and dead sorbents, respectively). The above comparison indicated that the pseudo-second-order kinetic parameters were more suitable for calculating the equilibrium adsorption capacity and removal rate.

**Isothermal adsorption characteristics**

The adsorption isotherm to some extent reflected the strength of interaction, surface properties, and affinity of the adsorbent for different heavy metal ions (Mohapatra et al. 2019). In this study, Langmuir, Freundlich, and D-R isotherm models were selected to simulate a favorable equilibrium uptake curve and reveal the adsorption behavior of living and dead cells *Paenibacillus* sp. LYX-1(Fig. 4). In the case of the Langmuir isotherm equation, the biosorption feature was determined by both \( q_{\text{max}} \), \( K_L \), and \( R_L \) value (Ranjan et al. 2009). As shown in Fig. 4c and Table 1, the regression coefficient \( R^2 \) of Langmuir and Freundlich equations were 0.9704 and 0.9915, respectively, indicating that these two models could describe the adsorption process of living biomass well. This result suggested that Cd\(^{2+}\) biosorption by living adsorbent was more likely to be monolayer and heterogeneous surface adsorption; besides, other intracellular accumulation mechanisms might be involved in the removal process of Cd\(^{2+}\) by living cells. In addition, the Langmuir model \( (R^2 = 0.9871) \) was more applicable to simulate the dead cell adsorption process than Freundlich \( (R^2 = 0.9478) \), indicating that the nature of biosorption by dead cells was a monolayer and non-heterogeneous adsorption. As seen in Table 1, the maximum adsorption capacity of living and dead cells for Cd\(^{2+}\) sorption, estimated from the Langmuir \( q_{\text{max}} \) parameter, was found to be 30.6790 mg/g and 24.3752 mg/g, respectively. The \( R_L \) values in this study were 0.0461 and 0.0310 for living and dead sorbent, respectively, which were between 0 and 1. The \( R_L \) values indicated that both living and dead biosorbents possessed a good affinity for Cd\(^{2+}\) (Won et al. 2010). The high adsorption properties of *Paenibacillus* sp. meant that it had a strong removal ability of Cd and might reduce the bioavailability of Cd\(^{2+}\) in the contaminated soil. Therefore, the biocontrol LYX-1 might control the migration of heavy metal pollutants into plants while exerting its biocontrol effect on the pathogenic bacterium.

For the D-R model, the plots of \( \ln q_e \) versus \( e^2 \) were shown in Fig. 4e, and parameters were presented in Table 1. Additionally, the magnitude of \( E \) might give useful information about the type of adsorption process (physical or chemical) (Ishola et al. 2014; Tran et al. 2016). Physical adsorption arises from relatively weak interactions such as van der Waals force, while chemical adsorption involves stronger chemical interactions (chemical bonding) with an attendant transfer of electrons between the adsorbent and adsorbate (Tran et al. 2017). In essence, the value of \( E \) for living and dead biomass was found to be in the range from 8 to 16 kJ/mol, indicating that chemisorption (ion exchange

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**Table 1** Kinetic parameters obtained for the adsorption of Cd\(^{2+}\) using the linear method and isothermal constants, coefficient of determination \( (R^2) \) for the models fitted to equilibrium Cd\(^{2+}\) biosorption onto biomass *Paenibacillus* sp. LYX-1 strain (data calculated by the equation of regression line obtained by software Origin 2018)

| Models                  | Parameters                  | Biosorbents     |
|-------------------------|-----------------------------|-----------------|
|                         |                             | Living biomass  | dead biomass |
| Pseudo-first-order kinetic | \( q_e, \text{exp} \) (mg/g) | 23.7158         | 20.5453      |
|                         | \( q_e, \text{cal} \) (mg/g) | 7.7250          | 5.7030       |
|                         | \( k_1 \) (min\(^{-1}\))    | 9.8338 \times 10^{-3} | 2.5930 \times 10^{-2} |
|                         | \( R^2 \)                   | 0.7273          | 0.7365       |
| Pseudo-second-order kinetic | \( q_e, \text{exp} \) (mg/g) | 23.7158         | 20.5453      |
|                         | \( q_e, \text{cal} \) (mg/g) | 23.3614         | 19.9568      |
|                         | \( k_2 \) (mg/g min)        | 8.5471 \times 10^{-3} | 1.5590 \times 10^{-2} |
|                         | \( R^2 \)                   | 0.9894          | 0.9798       |
| Langmuir               | \( q_{\text{max}} \) (mg/g) | 30.6790         | 24.3752      |
|                         | \( K_L \) (L/g)             | 0.4130          | 0.6244       |
|                         | \( R_L \)                   | 0.0461          | 0.0310       |
|                         | \( R^2 \)                   | 0.9704          | 0.9871       |
| Freundlich             | \( K_F \) (mg/g)            | 9.4936          | 8.2306       |
|                         | \( n \)                     | 3.48831         | 4.5157       |
|                         | \( R^2 \)                   | 0.9915          | 0.9378       |
| D-Riskubin-Redushkevich (D-R) | \( \beta \) (mol\(^2\)/kJ) | 2.6201 \times 10^{-9} | 2.7162 \times 10^{-9} |
|                         | \( E \) (kJ/mol)            | 13.8313         | 13.5676      |
|                         | \( R^2 \)                   | 0.9757          | 0.9065       |
complexation and precipitation) controlled the adsorption process.

**Desorption performance of strain LYX-1**

In order to determine the regeneration efficiency of both living and dead strain LYX-1 biosorbents, desorption experiments were conducted with 0.1 M HNO₃ and 0.1 M Na₂EDTA eluents respectively. Fig S3 showed that there was a difference in the desorption efficiency of different eluents for Cd²⁺ from strain LYX-1. In Fig. S4, 0.1 M HNO₃ could desorb 95.77% and 92.75% Cd²⁺ from living cells and dead cells, respectively. However, Na₂EDTA desorbed just 76.11% and 75.03% Cd²⁺ from living and dead cells, respectively. The above results indicated that 0.1 M HNO₃ had better performance than 0.1 M Na₂EDTA in desorbing the Cd²⁺ from both living and dead strain LYX-1, which was consistent with the study of Zhou et al. (2014). Hence, the results suggested that the adsorbed strain LYX-1 could be effectively desorbed. Thus, the high desorption efficiency of the adsorbed strain LYX-1 sorbents could not save the cost in practical application, but also, facilitate the recovery and utilization of Cd²⁺.

**Mechanisms of the Cd²⁺ biosorption by strain LYX-1**

**SEM–EDS analysis**

Based on the micro-characterization SEM–EDS study of biomass, Cd biosorption mechanisms by the strain *Paenibacillus* sp. LYX-1 was analyzed. Figure 5 showed surface characteristic changes of living and dead cells morphology before and after Cd²⁺ removal. We found that the surface of living cells appeared smooth and short-rod shapes, while living cells after absorbing Cd²⁺ became rough and ruptured, accompanied by a large amount of flocculent sedimentation (Fig. 5a and b). Compared with living cells, dead cells seemed to be rougher, which might be caused by temperature heat treatment (Fig. 5c).

![Fig. 5](image_url) Scanning electron micrograph (SEM) and energy dispersive spectrometer (EDS) of the a living cells without Cd²⁺ treatment; b living cells treated with 50 mg/L Cd²⁺, c dead cells without Cd²⁺ treatment, d dead cells treated with 50 mg/L Cd²⁺
After the biosorption of Cd, precipitated materials appeared on the surface of dead cells, indicating that numerous Cd\(^{2+}\) ions were adsorbed on the surface of dead biomass (Fig. 5d). The result indicated that strain LYX-1 could effectively realize the removal of Cd\(^{2+}\) in solution through precipitation during the process of Cd\(^{2+}\) biosorption. Besides, the EDS analysis further verified the adsorption of Cd\(^{2+}\) by the biosorbents. No Cd peaks were detected in pristine cells. However, the peaks of Cd\(^{2+}\) with all the other elements were detected in the EDS analysis of two biomass samples after Cd biosorption. Elemental variation of strain LYX-1 before and after biosorption was in Table S2. The presence of Cd on the cell surface after adsorption as seen from EDS images (Fig. 5b and d) proved the biosorption of Cd\(^{2+}\) by living and dead biosorbents of Paenibacillus sp. LYX-1.

**FTIR analysis**

In order to confirm the changes in functional groups involved in the Cd binding of biomass, the FTIR analysis was carried out. The FTIR spectrum of raw and Cd\(^{2+}\)-loaded living and dead biosorbent was presented in Fig. 6, where characteristic transmittance peaks listed were identified according to previous reports (Chen et al. 2012; Huang et al. 2016; Sun et al. 2020). For untreated living and dead cells, in Table S3, the peaks observed at 3429.88, 2923.73, 1647.93, 1544.78, 1236.90, 1069.97, and 672.87 (living) and 3413.90, 2921.66, 1643.37, 1540.02, 1245.74, 1054.21, and 633.56 (dead) were assigned to associated O–H, N–H, -CH\(_2\), amide I (-C=O/C-N), amide II (C-N/N–H), S\(^{2-}\), C-N and phosphate, or sulfate functional groups, respectively (Peng et al. 2020). The free Cd\(^{2+}\) could be fixed by the abundant oxygen-containing and amino functional groups via the formation of surface complexation, which could be described:

\[
\text{Cd}^{2+} + 2\text{OH}^- / \text{LYX} - 1 = \text{Cd(OH)}_2(s)/\text{LYX} - 1 \quad (10)
\]

\[
\text{Cd}^{2+} + \text{PO}_4^{3-} / \text{LYX} - 1 = \text{Cd}_2\text{(PO}_4)_2(s)/\text{LYX} - 1 \quad (11)
\]

\[
\text{Cd}^{2+} + -\text{CO} / \text{LYX} - 1 \rightarrow \text{Cd(CO)}_2^{2+}/\text{LYX} - 1 \quad (12)
\]

\[
\text{Cd}^{2+} + \text{COOH} / \text{LYX} - 1 \rightarrow \text{Cd(COO)}_2^{2+}/\text{LYX} - 1 + 2\text{H}^+ \quad (13)
\]

\[
\text{Cd}^{2+} + -\text{NH}_2 / \text{LYX} - 1 \rightarrow \text{Cd(NH}_2)_2^{2+}/\text{LYX} - 1 \quad (14)
\]

After Cd\(^{2+}\) biosorption, there was only a slight shift of groups between control and Cd\(^{2+}\) treated groups. However, attributed to the interaction between adsorbents and heavy metal, -OH, -NH, -CH\(_2\), -C = O, O = C-O, C-N, S\(^{2-}\), and phosphate functional groups were red or blue shifted when compared to nature living and dead cells, suggesting that those shifted bonds and correspond functional groups might be involved in Cd biosorption.

**XPS analysis**

Full-range XPS spectra of Paenibacillus sp. before and after biosorption are shown in Fig. 7a, which proved Cd\(^{2+}\) were adsorbed onto the strain LYX-1. The peaks of C-O at 286.31 eV and 286.39 eV (BE) of living and dead cells, respectively, were slightly reduced (Fig. 7b), which indicated that surface reducing groups such as C–OH could form precipitation with Cd\(^{2+}\) or provide protons to promote the formation of CO-Me (CO-Cd\(^{2+}\)) (Ho et al. 2017). By comparing the O 1 s spectra of the control and experimental groups, the peaks of O 1 s at 532.60 eV and 532.62 eV of living and dead cells were also considered as C-O-Cd\(^{2+}\) (Fig. 7c). Peaks of Cd detected after the adsorption could be divided into peaks at 405.39 eV and 411.98 eV, corresponding to Cd\(^{3d5/2}\) and Cd\(^{3d3/2}\) (Fig. 7d), respectively. There peaks (404.85 eV, 405.30 eV, 405.78 eV for living cells, 404.80 eV, 405.30 eV, and 405.78 eV for dead cells) could be possibly ascribed to Cd(OH)\(_2\), CdCO\(_3\), and CdS. Figure 7e and f also demonstrated the generation of CdS precipitation. XPS results also identified that chemisorption controlled the biosorption process of Cd\(^{2+}\) by LYX-1 (Fig. 4e).

**TEM analysis**

In order to further explore the contribution of intracellular bioaccumulation to Cd\(^{2+}\) removal during the biosorption process of the biocontrol strain LYX-1, TEM was used to...
observe the changes in bacterial surface morphology in the presence of Cd$^{2+}$. It could be seen from Fig. 8a that the living control cells were full of intracellular and had uniform cytoplasm, complete cell wall structure, and clear boundaries, which was consistent with the results of Bacillus cereus RC-1 and Pseudomonas sp. strain 375 (Huang et al. 2013). On the one hand, when under the stress of 50 mg/L Cd$^{2+}$, living biomass had a clear gap between the cell wall and cytoplasm of living biomass with high-density black particular matter appearing inside and outside the cell (Fig. 8b). This might be attributed to the contraction of the cytoplasm to increase the intracellular accumulation of Cd$^{2+}$ and form a resistance mechanism (Sun et al. 2020). Additionally, this also verified the results of the previous isotherm and kinetic experiments that not only fast surface adsorption occurred in living cells, but also relatively slow intracellular accumulation (Fig. 4). After the high-temperature heat treatment, the cytoplasm of dead cells severely shrank and appeared different size vacuoles (Fig. 8c), besides, Fig. 8d appeared high-density black particulate matter, indicating that the adsorption of Cd by dead cells was mainly concentrated on the outer edge and periplasmic space, which was consistent with Huang et al. (2013).

**Conclusions**

This study isolated and identified a novel biocontrol bacterium from soil, named Paenibacillus sp. LYX-1. Strain LYX-1 could resist 50 mg/L Cd$^{2+}$ and had the CzcD gene
responsible for Cd$^{2+}$ efflux. pH, initial Cd$^{2+}$ concentration, adsorbent dose, and contact time had significant effects on the biosorption and removal capacity of living and dead biomasses for Cd$^{2+}$. Besides, the removal capacity of living cells reached 90.39% at 20 mg/L Cd$^{2+}$. The pseudo-second-order kinetic model was more suitable to two biosorbents. The maximum biosorption capacity obtained was 30.6790 mg/g (living biomass) and 24.3752 mg/g (dead biomass), respectively. The $E$ value of two biomasses ranged from 8 to 16 kJ/mol, revealing that chemisorption controlled the biosorption of Cd$^{2+}$ by *Paenibacillus* sp. LYX-1. Moreover, 0.1 M HNO$_3$ eluent could desorb 95.77% and 92.75% Cd$^{2+}$ from living cells and dead biosorbent, respectively, indicating that strain LYX-1 had high regeneration efficiency. SEM–EDS analysis demonstrated that Cd$^{2+}$ was bound on the cell wall. Besides, FTIR and XPS analysis confirmed that -OH, -NH, -C=O, O=C-O, C-N, S$^{2-}$, and phosphate functional groups participated in the biosorption performance of strain LYX-1 for Cd$^{2+}$. TEM analysis further indicated that bioaccumulation played a key role in the removal of Cd$^{2+}$ by living strain LYX-1 during the biosorption process. In addition, strain LYX-1 might be a renewable biomaterial which exhibited the promising application to the removal of Cd$^{2+}$ in the Cd-contaminated environment. Besides, the application potential of *Paenibacillus* sp. LYX-1 in the Cd$^{2+}$-contaminated environment deserved further study in the future.

Fig. 8 Submicroscopic structures of *Paenibacillus* sp., LYX-1 a nature living cells, b 50 mg/L Cd$^{2+}$-loaded living cells, c dead cells, d 50 mg/L Cd$^{2+}$-loaded dead cells
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11356-022-20581-8.

Author contribution Yixin Luo, Min Liao, and Xiaomei Xie conceived the idea. Min Liao and Xiaomei Xie designed the research. Yixin Luo, Yuhao Zhang, Na Xu, Xiaomei Xie, and Qiyan Fan performed the experiment. Yixin Luo, Min Liao, and Xiaomei Xie analyzed the data and wrote the manuscript. All authors contributed to the discussion of the manuscript.

Funding This work was financially funded by the Nation Key Research and Development project of China and the National Natural Science Fund of China (grant number 2018YFC1800403, 41571226).

Data availability All data generated or analyzed during this study are included in this published article and its supplementary information files.

Declarations

Ethics approval This article does not contain any studies with human or animal subjects performed by either of the authors.

Consent to participate Not applicable.

Consent to publication All authors have read the submitted version of the manuscript and agree to submit the work to Environmental Science and Pollution Research, and we all agree that the transfer of copyright from the author to Environmental Science and Pollution Research.

Competing interest The authors declare no competing interests.

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