Diversity of cultivable endophytic bacteria associated with halophytes in Xinjiang of China and their plant beneficial traits postprint

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Abstract

Endophytic bacteria from halophytes have a wide range of application prospects in various fields, such as plant growth-promoting, biocontrol activity and stress resistance. The current study aimed to identify cultivable endophytic bacteria associated with halophytes grown in the salt-affected soil in Xinjiang Uygur Autonomous Region, China and to evaluate their plant beneficial traits and enzyme-producing activity. Endophytic bacteria were isolated from Reaumuria soongorica (PalL Maxim.), Artemisia carvifolia (Buch.-Ham. ex Roxb. Hort. Beng.), Peganum harmala L. and Suaeda dendroides (C. A. Mey. Moq.) by using the cultural-dependent method. Then we classified these bacteria based on the difference between their sequences of 16S rRNA (16S ribosomal RNA) gene. Results showed that the isolated bacteria from R. soongorica belonged to the genera Brucella, Bacillus and Variovorax. The bacteria from A. carvifolia belonged to the genera Micromonospora and Brucella. The bacteria from P. harmala belonged to the genera Paramesorhizobium, Bacillus and Peribacillus. The bacteria from S. dendroides belonged to the genus Bacillus. Notably, the genus Bacillus was detected in the three above plants, indicating that Bacillus is a common taxon of endophytic bacteria in halophytes. And, our results found that about 37.50% of the tested strains showed strong protease-producing activity, 6.25% of the tested strains showed strong cellulase-producing activity and 12.50% of the tested strains showed moderate lipase-producing activity. Besides, all isolated strains were positive for IAA (3-Indoleacetic acid) production, 31.25% of isolated strains exhibited a moderate phosphate solubilization activity and 50.00% of isolated strains exhibited a weak siderophore production activity. Our findings suggest that halophytes are valuable resources for identifying microbes with the ability to increase host plant growth and health in salt-affected soils.

Full Text

Diversity of Cultivable Endophytic Bacteria Associated with Halophytes in Xinjiang, China and Their Plant Beneficial Traits

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Abstract: Endophytic bacteria from halophytes have wide-ranging application prospects in fields such as plant growth promotion, biocontrol activity, and stress resistance. The current study aimed to identify cultivable endophytic bacteria associated with halophytes grown in salt-affected soils in Xinjiang Uygur Autonomous Region, China, and to evaluate their plant beneficial traits and enzyme-producing activity. Endophytic bacteria were isolated from *Reaumuria soongorica* (PalL Maxim.), *Artemisia carvifolia* (Buch.-Ham. ex Roxb. Hort. Beng.), *Peganum harmala* L., and *Suaeda dendroides* (C. A. Mey. Moq.) using culture-dependent methods and classified based on 16S rRNA gene sequences. Results showed that bacteria isolated from *R. soongorica* belonged to the genera *Brucella*, *Bacillus*, and *Variovorax*; those from *A. carvifolia* belonged to *Micromonospora* and *Brucella*; those from *P. harmala* belonged to *Parameshorhizobium*, *Bacillus*, and *Peribacillus*; and those from *S. dendroides* belonged to *Bacillus*. Notably, the genus *Bacillus* was detected in three of the four plants, indicating that it is a common taxon of endophytic bacteria in halophytes. Approximately 37.50% of tested strains showed strong protease-producing activity, 6.25% showed strong cellulase-producing activity, and 12.50% showed moderate lipase-producing activity. All isolated strains were positive for IAA (3-Indoleacetic acid) production, 31.25% exhibited moderate phosphate solubilization activity, and 50.00% exhibited weak siderophore production activity. These findings suggest that halophytes are valuable resources for identifying microbes capable of enhancing host plant growth and health in salt-affected soils.

Keywords: endophytes; environmental microbiology; halophytes; biodiversity; plant beneficial properties

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1 Introduction

The Xinjiang Uygur Autonomous Region possesses the largest land area in China, accounting for approximately one-sixth of the nation's total territory (Li et al., 2004). However, most of this land is covered by deserts and saline-alkali soils (Huang et al., 2006). Furthermore, with the continuous expansion of agriculture and frequent human disturbance, problems of soil desertification and salinization have become increasingly severe, posing significant environmental challenges (Hu et al., 2012; Jiang et al., 2020).

Halophytes can survive in highly saline and arid soils while obtaining substantial biomass, giving them great economic value and ecological significance for restoring vegetation in saline soils, improving soil biodiversity, and increasing crop productivity (Shamsutdinov et al., 2017). Endophytes are non-pathogenic microorganisms that reside in the tissues and organs of healthy plants during certain or all growth stages, including endophytic bacteria, actinomycetes, and fungi (Tosi et al., 2021). While both endophytic actinomycetes and bacteria belong to the bacterial kingdom of prokaryotes taxonomically, they differ morphologically: actinomycetes typically exhibit filamentous cell morphology with dense, difficult-to-collect colonies, whereas bacteria are generally spherical or rod-shaped with round, easily collected colonies. Both represent important bio-resources associated with plants, as most endophytes promote host plant growth, enhance nutrient acquisition, and improve tolerance to abiotic stresses such as drought, salinity, and other environmental pressures (Farahat, 2020). Evidence also indicates coevolution between endophytes and halophytes (Khare et al., 2018; Taulé et al., 2021), wherein host plants provide suitable living environments and abundant nutrients for endophytes, while endophytes promote host plant growth through nitrogen fixation, auxin release, and other secondary metabolites (Wani et al., 2015; Afzal et al., 2019).

Recent studies have documented endophytic bacteria associated with halophytes. Using next-generation sequencing, Zhao et al. (2016a) identified Tenericutes, Proteobacteria, Firmicutes, and Actinobacteria as the main endophytic bacterial communities in sixteen halophytes from Northern Xinjiang. Zhao et al. (2016b) similarly found Proteobacteria, Bacteroidetes, Firmicutes, and Actinobacteria as the dominant endophytic bacterial communities in *Salicornia europaea* L. roots based on high-throughput sequencing analysis. Beyond their high diversity, halophyte endophytic bacteria can promote host plant growth. Teng et al. (2010) isolated four ACC (1-aminocyclopropane-1-carboxylate) deaminase-containing endophytic bacterial strains from *Suaeda glauca* (Bunge) Bunge, identified as *Pseudomonas* sp., *Pseudomonas oryzihabitans*, *Pseudomonas putida*, and *Pantoea agglomerans*. Khan et al. (2020) screened six isolates from fifty-nine endophytic bacterial isolates that significantly increased rice production.

Zhao et al. (2016c) identified five isolates associated with *S. europaea* that significantly stimulated host plant growth, recognized as *Variovorax paradoxus*, *Bacillus endophyticus*, *Bacillus tequilensis*, *Arthrobacter agilis*, and *Planococcus rifietoensis*. Sgroy et al. (2009) isolated twenty-nine endophytic bacterial strains from *Prosopis strombulifera* capable of producing phytohormones, with six tested isolates positive for ACC deaminase activity and one strain able to produce siderophores, though none could solubilize phosphate. Despite the many halophyte species in arid regions worldwide, the community composition and ecological roles of their associated endophytic bacteria remain poorly understood (Zhao et al., 2013).

This research investigated the community composition of cultivable endophytic bacteria associated with four halophytes collected from salt-affected soils in Xinjiang, China, along with their plant beneficial traits. The study aims were to: (1) isolate endophytic bacteria from four halophytes grown in saline-alkali soils; (2) identify the isolated endophytic bacteria via 16S rRNA gene sequencing; and (3) examine their plant beneficial traits.

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2 Materials and Methods

2.1 Plant Sample Collection and Pretreatment

Four halophytes—*R. soongorica* (Tamaricaceae), *A. carvifolia* (Asteraceae), *P. harmala* (Nitrariaceae), and *S. dendroides* (Amaranthaceae)—were collected from saline-alkali soils in Fukang City, Xinjiang, China (44°13 39 N, 87°40 16 E). These plants were designated P1, P2, P3, and P4, respectively. Samples were collected from their natural habitats, placed in sterile sampling bags, and transported to the laboratory. Each sample was flushed with running water to dislodge soil and mud from root surfaces and dust from plant surfaces, then surface-sterilized by sequential soaking in 75% medical alcohol for 5 minutes and 5% NaClO for 8 minutes, followed by three washes with sterile distilled water (Liu et al., 2017). Sterilization efficiency was verified by spreading 100 L of the final rinse water onto Tryptic Soy Agar (TSA) and International Streptomyces Project Medium (ISP2) agar plates. Absence of colony growth after 3 days of incubation at 30°C confirmed effective surface sterilization (Rajivgandhi et al., 2018; Ramachandran et al., 2019). Surface-sterilized plants were cut into 1–2 cm pieces with a sterile scalpel, dried in a horizontal flow clean bench, crushed with a sterile masher, and stored at -20°C.

2.2 Isolation of Endophytic Bacterial Strains

One gram of plant sample was ground thoroughly with a sterile mortar, transferred to a 50 mL centrifuge tube containing 9 mL sterile distilled water and a few sterile glass beads, and shaken at 100 r/min for 30 minutes using a Shaken

Incubator (Shanghai Tensuc Lab Instruments Manufacturing Co., Ltd., China). The tissue homogenate was centrifuged at 3000 r/min for 10 minutes, and the supernatant was transferred to a new sterile centrifuge tube. Serial gradient dilutions (10^{-2}-10^{-4}) were prepared aseptically, and 70 L aliquots were spread onto tap water-yeast extract agar (TWYE) medium and Glycerol-Asparagine medium. All plates were incubated at 30°C for 30 days. TWYE medium contained 0.25 g/L yeast extract, 0.5 g/L K_2HPO_4, 15 g/L agar, pH 7.2 (Wang, 2017). Glycerol-Asparagine medium contained 1 g/L asparagine, 10 g/L glycerol, 30 g/L NaCl, 1 g/L K_2HPO_4, 0.001 g/L $FeSO_4 \cdot 7H_2O$, 0.001 g/L $MnSO_4 \cdot H_2O$, 0.001 g/L $ZnSO_4 \cdot 7H_2O$, 15 g/L agar, pH 7.2 (Liao, 1997). After 30 days, colonies with different shapes and colors were carefully selected, transferred to TSA plates, and incubated at 30°C for 7 days to verify purity. Colonies with similar phenotypes (size, shape, and color) were duplicated to reduce the number of bacteria requiring sequencing and narrow the screening scope. Isolated strains were preserved in 20% glycerol tubes at -80°C.

2.3 DNA Extraction

Genomic DNA was extracted using Chelex® 100 sodium. A single colony was transferred to a sterile polymerase chain reaction (PCR) tube with 50 L of 5% Chelex-100, mixed thoroughly with a vortex mixer, incubated at 99°C for 25 minutes in a PCR instrument (C1000 Touch™ Thermal Cycler, Bio-Rad Laboratories, USA), and centrifuged at 12,000 r/min for 10 minutes. The extracted genomic DNA in the supernatant served as PCR template.

2.4 PCR and Agarose Gel Electrophoresis

The 16S rRNA gene was amplified using universal primers 27F (5' -GAGTTTGATCCTGGCTCAG-3') and 1492R (5'-GAAAGGAGGTGATCCAGCC-3') (Biomed, China). Amplification was performed in a C1000 Touch™ Thermal Cycler (Bio-Rad Laboratories, USA) in 50 µL reaction mixtures containing 1 µL template DNA, 25 µL 2×Taq MasterMix (Coolaber, China), 1 µL 27F, 1 µL 1492R, and 22 µL ddH_2O (Tiangen Biotech Co. Ltd., Beijing, China). PCR conditions were: pre-denaturation at 94°C for 6 minutes; 35 cycles of denaturation at 94°C for 30 seconds, annealing at 55°C for 30 seconds, and extension at 72°C for 1.5 minutes; final extension at 72°C for 7 minutes. Products of approximately 1500 bp were verified by 1% agarose gel electrophoresis.

2.5 Sequencing and Phylogenetic Tree Construction

Positive PCR products were purified and sequenced by Sangon Biotech in Shanghai, China. Paired-end raw data were merged using Molecular Evolutionary Genetics Analysis 7.0 (MEGA 7.0) and compared with strains in the EzBioCloud database using a 16S-based identification system. Isolate sequences were multiply aligned with the most similar sequences downloaded from EzBioCloud using the ClustalW method, and an evolutionary tree was constructed using the Neighbor-Joining method in MEGA 7.0.

2.6 Accession Numbers

All endophytic bacterial 16S rRNA gene sequences were deposited in GenBank under accession numbers MW228433–MW228448.

2.7 Plant Beneficial Traits

IAA production was assayed by color reaction (Amaresan et al., 2012). Strains were inoculated in nutrient broth and shaken (120 r/min) at 30°C for 5 days. Culture supernatant was collected after centrifugation at 5000 r/min for 10 minutes. Two milliliters of supernatant were mixed with 4 mL Salkowski reagent and incubated at 30°C for 30 minutes in darkness; pink or red coloration indicated IAA production.

Phosphate solubilization activity was measured by inoculating strains on Pikovskaya medium and incubating at 30°C for 5 days (Simarmata et al., 2020). The medium contained 0.5 g/L yeast extract, 10 g/L glucose, 5 g/L $Ca_3(PO_4)_2$, 0.5 g/L $(NH_4)_2SO_4$, 0.2 g/L NaCl, 0.2 g/L KCl, 0.1 g/L $MgSO_4 \cdot 7H_2O$, 0.025 g/L bromophenol blue, 0.002 g/L $FeSO_4 \cdot 7H_2O$, 20 g/L agar, pH 7.0. A transparent zone around colonies indicated phosphate solubilization.

Siderophore production was assessed by inoculating strains on Chrome Azurol S (CAS) agar plates and incubating at 30°C for 5 days. An orange or purple halo zone around colonies with color change in the blue CAS medium indicated positive siderophore production (Khan et al., 2020).

Protease activity was determined by growing isolates on Skim Milk Agar. Positive results showed a transparent halo region around bacterial colonies after 3 days at 30°C (Simarmata et al., 2020).

Cellulase activity was tested by inoculating isolates onto medium containing carboxymethyl cellulose sodium salt (CMC-Na). After 7 days at 30°C, plates were stained with 5 mL 0.1% Congo red solution for 10 minutes, then rinsed with 5 mL 1 M NaCl. A transparent or lightly colored region around colonies indicated positive cellulase activity (Simarmata et al., 2020).

Lipase activity was assayed by streaking isolates on Tween 80 medium containing 10 mL/L Tween 80, 50 mL/L Victoria blue suspension, 10 g/L peptone, 5 g/L NaCl, 0.1 g/L $CaCl_2 \cdot 7H_2O$, and 15 g/L agar. After 7 days at 30°C, clear halo formation indicated positive results (Mesa et al., 2015). Enzyme-producing activity was calculated using the formula (averaged from three replicates) (Liu et al., 2017):

$$E = \frac{D_1}{D_2}$$

where E is enzyme-producing activity, D_1 is the diameter of the clear zone (mm), and D_2 is the diameter of the bacterial colony (mm).

2.8 Data Processing and Visualization

Data processing and visualization were completed using Microsoft Excel 2019, MEGA 7.0, and GENESCLOUD (https://www.genescloud.cn/). Microsoft Excel 2019 was used for data processing and pie chart generation, MEGA 7.0 for phylogenetic tree construction, and GENESCLOUD for Venn diagram drawing.

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3 Results

3.1 Isolation and Identification of Endophytic Bacterial Strains

A total of sixteen endophytic bacterial strains belonging to three phyla, four classes, four orders, four families, and six genera were isolated from four halophytic plants. Table 1 shows 16S rRNA gene sequence similarities between isolated strains and the most closely related sequences in the EzBioCloud database. All independent isolates shared 98%–100% 16S rRNA gene similarity with database entries. The predominant genera were *Bacillus*, *Brucella*, and *Phyllobacterium*, accounting for 38%, 25%, and 19% of total isolates, respectively (Fig. 1 [Figure 1: see original paper]). Five isolates (P1.1–1.5) were obtained from P1, three (P2.1–2.3) from P2, five (P3.1–3.5) from P3, and three (P4.1–4.3) from P4. However, the Venn diagram in Figure 1b shows no endophytic bacteria common to all four halophytes.

Three phyla were represented among isolates: Actinobacteria (P2.1), Proteobacteria (P1.3–P1.5, P2.2, P2.3, P3.2, P3.3, P3.5), and Firmicutes (P1.1, P1.2, P3.1, P3.4, P4.1–P4.3). Isolates were identified as *Bacillus atrophaeus* (P1.2, P4.2, P4.3), *Bacillus filamentosus* (P3.1, P4.1), *Bacillus halotolerans* (P1.1), *Brevibacterium frigoritolerans* (P3.4), *Brucella endophytica* (P1.3, P1.5, P2.2, P2.3), *Micromonospora citrea* (P2.1), *Phyllobacterium phragmitis* (P3.2, P3.3, P3.5), and *Variovorax paradoxus* (P1.4) (Table 1; Fig. 2 [Figure 2: see original paper]). Although eight isolates (P1.3–P1.5, P2.2, P2.3, P3.2, P3.3, P3.5) belonged to Proteobacteria, they represented different classes: Alphaproteobacteria (P1.3, P1.5, P2.2, P2.3, P3.2, P3.3, P3.5) and Betaproteobacteria (P1.4; Table 1). Six Firmicutes isolates belonged to *Bacillus* and one to *Peribacillus* (Table 1; Fig. 1). The single actinomycete strain (P2.1) from P2 belonged to *Micromonospora* (Table 1; Fig. 2). At the species level, Firmicutes (four species) had more isolates than Proteobacteria (three species) and Actinobacteria (one species) across the four halophytes (Table 1; Fig. 2). The phylogenetic tree revealed the closest species matches for isolated endophytic bacterial strains in the EzBioCloud database (Fig. 2). Based on species diversity, Firmicutes representatives (4 species) were most abundant, followed by Proteobacteria (3 isolates) and Actinomycetes (1 isolate) in halophytes (Fig. 2).

3.2 Plant Beneficial Traits

Enzyme-producing activities were screened for sixteen endophytic bacterial strains from four halophytes. The highest protease activity was observed in isolates P1.1, P1.2, P3.3, P3.4, P4.2, and P4.3, while other isolates showed moderate or no activity (Table 2). Strong cellulase-producing activity was observed only in isolate P1.1, with 31.25% of tested strains showing negative cellulase activity (Table 2). Approximately 18.75% of strains exhibited lipase activity (Table 2).

All test isolates produced IAA, with strain P4.3 showing higher IAA production activity than others (Table 2). Isolates P1.4, P2.3, P3.1, P3.2, and P4.2 showed moderate phosphate solubilization activity, while P1.1, P1.2, P2.2, P3.3, P3.4, and P4.3 showed weak activity. Isolates P1.3, P1.5, P2.1, P3.5, and P4.1 showed no phosphate solubilization activity (Table 2). Half of all isolated strains weakly produced siderophores (Table 2). Notably, strain P1.1 produced all three tested enzymes, while isolates P1.2, P1.4, P2.3, P3.2, P3.3, and P3.4 could produce IAA, siderophores, and solubilize phosphate (Table 2), indicating their potential to promote host plant growth.

In protease screening, 37.50% of strains showed strong activity, 25.00% moderate activity, and 37.50% no activity (Fig. 3a [Figure 3: see original paper]). In lipase screening, 12.50% showed moderate activity, 6.25% weak activity, and 81.25% no activity (Fig. 3b). In cellulase screening, 6.25% showed strong activity, 31.25% moderate activity, 31.25% weak activity, and 31.25% no activity (Fig. 3c). For IAA production, 6.25% of strains showed moderate activity and 93.75% weak activity (Fig. 3d). In phosphate solubilization, 31.25% showed moderate ability, 37.50% weak ability, and 31.25% no ability (Fig. 3e). For siderophore production, 50.00% displayed weak activity and 50.00% showed none (Fig. 3f).

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4 Discussion

Global climate change has made soil salinization one of the most serious abiotic stresses affecting plant growth and crop production worldwide (Nakbanpote et al., 2014). Plant-associated endophytic bacteria reside in plant tissues throughout their lives and benefit host plant health and growth (Mishra et al., 2017; Fouda et al., 2021). By producing metabolites analogous to those released by host plants, endophytic bacteria represent a rich source of secondary metabolites (Gouda et al., 2016). To better understand the community structure and ecological roles of endophytic bacteria associated with halophytes, we selected four typical halophytes for isolation and functional screening.

Few studies have examined endophytic bacteria associated with *R. soongorica*, *A. carvifolia*, and *S. dendroides*. Using culture-dependent approaches, we isolated endophytic bacterial strains from four halophytes. Seven of sixteen isolates belonged to Firmicutes: *Bacillus halotolerans* (P1.1), *Brevibacterium frigoritol-*

erans (P3.4), *Bacillus endophyticus* (P4.1), *Bacillus filamentosus* (P3.1, P4.1), and *Bacillus atrophaeus* (P1.2, P4.2, P4.3) (Table 1). We also isolated an endophytic actinomycete, *Micromonospora citrea* (Table 1). The Proteobacteria phylum contained eight isolates in genera *Brucella*, *Paramesorhizobium*, and *Variovorax*: *Variovorax paradoxus* (P1.4), *Phyllobacterium phragmitis* (P3.2, P3.3, P3.5), and *Brucella endophytica* (P1.3, P1.5, P2.2, P2.3) (Table 1). Lei et al. (2020) previously isolated a novel Gram-positive, aerobic, motile endophytic actinomycete, *Actinokineospora pegani* sp. nov., from *Peganum harmala* roots.

Our findings revealed that *Bacillus halotolerans* (P1.1) can produce protease, cellulase, lipase, IAA, and solubilize phosphate (Table 2). Previous research showed that inoculation with *Bacillus halotolerans* significantly enhanced plant development, nutritional content, and food quality even under saline stress (Jiménez-Gómez et al., 2021). Our isolates also demonstrated plant growth-promoting traits such as IAA production and phosphate solubilization (Table 2). *Bacillus atrophaeus* (P1.2, P4.3) produced protease and lipase, consistent with Mohamad et al. (2018), and also possessed plant growth-promoting potential (Table 2).

Strains P1.3, P1.5, P2.2, and P2.3 were identified as *Brucella endophytica*; notably, the basonym of *Brucella endophytica* is *Ochrobactrum endophyticum*. A similar investigation proposed *O. endophyticum* as an endophytic bacterium isolated from *Glycyrrhiza uralensis* F. roots (Li et al., 2016). Few studies have examined the plant growth-promoting potential and enzyme-producing activity of *B. endophytica*, but our findings indicate it possesses certain plant beneficial traits and cellulase production capability (Table 2). Strain P1.4, isolated from *R. soongorica* and identified as *Variovorax paradoxus*, could produce IAA, siderophores, and solubilize phosphate, suggesting it may promote host plant growth under certain conditions (Tables 1 and 2). Chen et al. (2013) demonstrated that *V. paradoxus* containing ACC deaminase can promote *Arabidopsis thaliana* growth.

Isolate P2.1, identified as *Micromonospora citrea* (phylum Actinobacteria), was previously shown to produce a novel family of antibacterial antibiotics (Carter et al., 1990). However, no reports exist on its plant beneficial traits; our results show it can produce protease, cellulase, and IAA (Table 2). Three endophytic strains with plant beneficial traits were isolated from *P. harmala* (P3) growing in saline soils and identified as *Phyllobacterium phragmitis*. These Gram-negative bacteria were first isolated from *Phragmites australis* rhizomes in the Kumtag Desert (Liang et al., 2019). While no previous references describe plant beneficial traits of *P. phragmitis*, we found it can produce IAA and siderophores, indicating growth-promoting potential (Table 2). Isolate P3.4, identified as *Brevibacterium frigoritolerans*, showed plant growth-promoting traits and strong protease activity. Unnisa et al. (2021) similarly found *B. frigoritolerans* has plant growth promotion potential (phosphate solubilization, IAA and ammonia production) and biocontrol properties (hydrogen cyanide and siderophore production, lytic enzymes). Strains P3.1 and P4.1, identified as *Bacillus fila-*

mentosus, exhibited cellulase activity and IAA production capability (Table 2). Yahaghi et al. (2019) found *B. filamentosus* most effective in stimulating alfalfa seedling root and shoot growth. To our knowledge, few reports describe *B. filamentosus* isolation from plants, particularly halophytes, though it was first isolated from marine sediment (Sonalkar et al., 2015).

5 Conclusions

Sixteen endophytic bacteria associated with halophytes were isolated, belonging to genera *Bacillus*, *Micromonospora*, *Brucella*, *Paramesorhizobium*, *Peribacillus*, and *Variovorax*. All isolates produced IAA, and some were positive for production of the three tested enzymes, siderophores, and phosphate solubilization. These endophytic bacteria play important roles in promoting host plant growth and improving stress resistance. Our findings indicate that halophytes serve as a resource bank for functional microbes that can sustain plant health and growth under harsh climates. Application of functional endophytes in agricultural production thus holds great economic value and ecological significance. Further laboratory and field studies are needed to confirm the plant growth-promoting traits of endophytic bacteria isolated from halophytes.

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Note: Figure translations are in progress. See original paper for figures.