Endophytic Microbial Community Composition and Function in Haloxylon ammodendron Seeds (Postprint)

Authors: Zhu Chaohua, Zhai Yixiao, Xinrong Li, Miao Yingxiang, Ma Tong, Li Shanjia

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Abstract

To reveal the ecological adaptation mechanisms and plant growth-promoting potential of seed endophytic microorganisms in desert plants, this study investigated the seeds of the xerophytic plant Haloxylon ammodendron, combining high-throughput sequencing and traditional culture techniques to uncover the community structure characteristics and plant growth-promoting and stress resistance potential of its endophytic microorganisms. The results showed that endophytic bacteria in H. ammodendron seeds encompassed 31 phyla and 668 species, with the dominant phyla being Firmicutes and Bacteroidetes; endophytic fungi involved 13 phyla and 583 species, with the dominant phyla being Ascomycota and Basidiomycota. Functional annotation revealed the division of labor characteristics of these endophytic microorganisms: endophytic bacteria were primarily chemoheterotrophic and fermentation functions, while the endophytic fungal community exhibited functional differentiation between saprotrophic and pathogenic roles. Conventional culture methods screened 13 culturable endophytic bacterial strains, including two multifunctional plant growth-promoting bacteria (Priestia aryabhattai HB-4, Priestia megaterium HB-9) and three salt-alkali tolerant strains (Bacillus zhangzhouensis HB-6, Bacillus safensis HB-10, and Bacillus pumilus HB-11). Experimental results demonstrated that strains HB-4 and HB-9 could promote wheat growth; strains HB-6, HB-10, and HB-11 could alleviate the inhibition of wheat growth caused by salt-alkali stress. This study reveals the ecological functional characteristics of endophytic microorganisms in H. ammodendron seeds, providing new insights for microbial resource mining in desert ecosystems and the development of plant growth-promoting microbial agents.

Full Text

Community Composition and Functionalities of Endophytic Microorganisms in *Haloxylon ammodendron* Seeds

ZHU Zhaohua, ZHAI Yixiao, LI Xinrong, MIAO Yingxiang, MA Tong, LI Shanjia
(School of Life Science and Engineering, Lanzhou University of Technology, Lanzhou 730050, Gansu, China)

Abstract

To elucidate the ecological adaptation mechanisms and growth-promoting potential of endophytic microorganisms in desert plant seeds, this study investigated the xerophytic plant *Haloxylon ammodendron* using high-throughput sequencing combined with traditional culture techniques. The results revealed that endophytic bacteria in *H. ammodendron* seeds encompassed 668 species across 31 phyla, with Firmicutes and Bacteroidetes as the dominant phyla. Endophytic fungi comprised 583 species across 13 phyla, dominated by Ascomycota and Basidiomycota. Functional annotation demonstrated distinct metabolic roles: endophytic bacteria were primarily enriched in chemoheterotrophy and fermentation, while fungal communities exhibited functional differentiation between saprophytic and pathogenic traits. Conventional culture methods isolated 13 culturable endophytic bacterial strains, including two multifunctional plant growth-promoting strains (*Priestia aryabhattai* HB-4 and *Priestia megaterium* HB-9) and three salt-alkaline tolerant strains (*Bacillus zhangzhouensis* HB-6, *Bacillus safensis* HB-10, and *Bacillus pumilus* HB-11). Pot experiments demonstrated that strains HB-4 and HB-9 significantly promoted wheat growth, while strains HB-10 and HB-11 alleviated saline-alkaline stress-induced growth inhibition in wheat. This study illuminates the ecological functional characteristics of endophytic microorganisms in desert plant seeds, providing novel insights for microbial resource exploitation in desert ecosystems and the development of plant growth-promoting microbial agents.

Keywords: *Haloxylon ammodendron* seeds; endophytic microorganisms; community structure; diversity; growth-promoting bacteria

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Introduction

Endophytic microorganisms reside within plant tissues without causing harm to their hosts, typically colonizing above-ground parts, roots, and seeds. During host plant growth, endophytic microorganisms participate in physiological metabolic regulation through various interaction mechanisms, promoting plant development and becoming an indispensable tool in modern agricultural production with broad application prospects. Seed endophytic microorganisms and host plants mutually influence each other, playing positive roles in improving

nutrition and helping plants resist biotic and abiotic stresses. On one hand, they effectively facilitate nutrient transfer from soil to plants, promoting growth while enhancing disease resistance and stress tolerance. Their mechanisms of action are primarily manifested in two aspects: (1) direct promotion of plant growth through indole-3-acetic acid (IAA) secretion, biological nitrogen fixation, phosphorus solubilization, and siderophore synthesis; and (2) assistance in resisting pests, diseases, and environmental stress by secreting hydrolytic enzymes (such as chitinases and cellulases), synthesizing antagonistic substances (alkaloids, volatile organic compounds), and inducing plant resistance gene expression.

Seeds, as important plant reproductive organs, contain substantial genetic material and serve as stable microbial carriers and reservoirs due to their long-term dormancy. Seeds harbor rich endophytic microbial communities that play crucial roles in promoting seed germination and ensuring healthy seedling growth. For example, endophytic microbial communities in *Astragalus* seeds promote germination by suppressing pathogens and degrading cellulose, while rice seed microbiomes collectively benefit early rice growth. Common culturable seed endophytic bacteria include *Azoarcus*, *Bacillus*, *Pseudomonas*, *Paenibacillus*, and *Pantoea*, while seed endophytic fungi primarily include *Fusarium*, *Aspergillus*, *Alternaria*, *Penicillium*, *Cladopsorium*, *Colletotrichum*, and *Talaromyces*. Endophytic fungi exhibit similar functions, enabling cucumber and tomato to effectively resist drought and salt stress under the mediation of salt-tolerant endophytic fungi. *Trichoderma* enhances host plant disease resistance by antagonizing pathogens and competing for ecological niches and nutritional resources. On the other hand, host plants selectively recruit beneficial microorganisms from the environment to colonize themselves. These microorganisms exhibit dynamic changes, with their community structure regulated not only by the host plant but also potentially influenced by abiotic factors such as water sources, soil, geography, and climate. In contrast, seed endophytic microorganisms typically colonize through horizontal and vertical transmission, with certain dominant strains stably inherited across generations through seeds, forming long-term mutualistic relationships with host plants. Therefore, in-depth research on seed endophytic microbial community composition, functional diversity, and their synergistic mechanisms with plants is significant for promoting sustainable agricultural development.

Haloxylon ammodendron is a perennial desert shrub widely distributed in northwestern China. As a key species in desert ecosystems, *H. ammodendron* plays important roles in windbreak and sand fixation, soil improvement, and biodiversity maintenance. Recent research on *H. ammodendron* has primarily focused on drought resistance and saline-alkaline tolerance physiological characteristics, while studies on its endophytic microorganisms remain relatively scarce. Although previous studies have systematically reviewed the diversity and functions of desert plant endophytic microorganisms, research on the community structure and function of endophytic microorganisms in seeds, a special microenvironment, is still lacking. Therefore, this study employed *H. ammodendron* seeds as ma-

terial, using a strategy combining high-throughput sequencing and traditional culture to comprehensively analyze the community structure and function of its endophytic microorganisms. Based on this, isolated strains were evaluated for growth-promoting and saline-alkaline tolerance functions. The results not only clarify the key roles of seed endophytic microorganisms in environmental adaptation of desert plants and provide theoretical basis for microbial resource exploitation, but also establish a scientific foundation for developing novel microbial agents based on "plant-microbe" interaction mechanisms.

Materials and Methods

Sample Collection and Preparation

Test samples were collected from *H. ammodendron* seeds in Minqin County, Wuwei City, Gansu Province (38°35 N, 102°58 E). After collection, samples were placed in self-sealing bags, numbered, and stored at -80°C for long-term preservation for endophytic microbial analysis.

Culture Media

Culture media for isolating endophytic microorganisms included Ashby medium (nitrogen-free), Gause' s No. 1 medium, and NBRIP medium. Nitrogen fixation experiments used Ashby medium, phosphorus solubilization experiments used NBRIP medium, and siderophore production experiments used Chrome Azurol S (CAS) medium. Salt and alkaline tolerance screening was performed on LB medium supplemented with different NaCl or $NaHCO_3$ concentrations.

Seed Surface Sterilization and DNA Extraction

Healthy, plump seeds were weighed and surface-sterilized by washing with sterile water three times to remove surface dust, followed by treatment with 2.5% NaClO for 3 min, then 75% ethanol for 3 min, and finally rinsed with sterile water 7-8 times. To verify sterilization effectiveness, 100 L of the final rinse water was plated on fresh medium and incubated for 2-7 days; no colony growth confirmed complete sterilization. After surface sterilization, seeds were snap-frozen in liquid nitrogen for 2-3 h and stored at -80°C, with four biological replicates per sample. Samples were transported on dry ice to Biomarker Technologies Co., Ltd. (Beijing) for DNA extraction using the TGuide S96 Magnetic Soil/Stool DNA Kit (Tiangen Biotech). After concentration verification, libraries were constructed and sequenced using the Illumina NovaSeq6000 platform. Raw sequencing data were uploaded to the NCBI database with accession numbers PRJNA1202999 (bacteria) and PRJNA1204448 (fungi).

High-Throughput Sequencing and Data Analysis

Bacterial 16S rRNA genes were amplified using primers 5 -CADACTCCTACGGGAGGC-3 and 5 -ATCCTGTTTGMTMCCCVCR-3 . Fungal ITS regions were amplified using primers ITS1F (5 -CTTGGTCATTTAGAGGAAGTAA-3) and ITS2R (5 -TGCGTTCTTCATCGATGC-3). PCR products were detected by agarose gel electrophoresis, purified using the Monarch DNA Gel Extraction Kit, and subjected to high-throughput sequencing. Sequencing data were analyzed using the BMKCloud platform (Biomarker Technologies) for bacterial and fungal community composition, α-diversity, and functional prediction analysis.

Isolation and Identification of Endophytic Bacteria

After surface sterilization, plump seeds were selected and inoculated onto isolation media, incubated at 30°C for 2-7 days. Remaining seeds were ground in 10 mL sterile water, serially diluted to 10^{-3}, and 50 L of supernatant was plated onto various media. After incubation at 30°C for 2-7 days, colonies with different morphologies were selected and purified 3-5 times until morphology, size, and color were consistent. Identification was performed by 16S rRNA gene sequencing. Genomic DNA was extracted using a column-based bacterial genome extraction kit. PCR amplification was performed using universal primers 27F (5 -AGAGTTTGATCCTGGCTCAG-3) and 1492R (5 -TACGGCTACCTTGTTACGACTT-3) in a 20 L reaction containing 8 L 2×Taq PCR Mix, 1 L each primer, and 1 L template. The PCR program consisted of initial denaturation at 95°C for 5 min, followed by 30 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 1 min, with a final extension at 72°C for 10 min. Products were verified by agarose gel electrophoresis and sequenced by Genewiz (Suzhou, Jiangsu). Sequences were compared against the NCBI database for taxonomic identification and uploaded to GenBank.

Functional Screening of Endophytic Bacteria

Qualitative and quantitative screening was performed for various plant growth-promoting traits. IAA production was quantified using the Salkowski method, with positive strains selected for OD_{530} measurement and concentration calculated using the standard curve $y = 0.0251x + 0.0997$ ($R^2 = 0.9971$). Nitrogen fixation was screened on Ashby nitrogen-free medium, phosphorus solubilization on NBRIP medium, and siderophore production on CAS medium. Salt and alkaline tolerance was screened by streaking on LB medium supplemented with different concentrations of NaCl or $NaHCO_3$.

Pot Experiments

Growth-promoting pot experiments were conducted in a greenhouse using wheat cultivar “Jimai 22”. Each pot contained 0.5 L of sterilized substrate (nutrient soil and vermiculite mixed 2:1, v/v) autoclaved at 121°C for 45 min. Wheat seeds were surface-sterilized, soaked in sterile water for 12 h, and germinated in sterile

vermiculite. Uniform seedlings were transplanted to pots (4 plants per pot, 15 replicates per treatment). Strains *P. aryabhattai* HB-4 and *P. megaterium* HB-9 were cultured in LB liquid medium at 180 $r \cdot min^{-1}$ to logarithmic phase, harvested by centrifugation at 5000 $r \cdot min^{-1}$ for 10 min, and resuspended in sterile water to $OD_{600} = 1.0$. The bacterial suspension (20 mL) was evenly applied around wheat roots, with sterile water as control. Applications were performed once at transplanting and again 15 days later. Plants were harvested 30 days after transplanting for physiological and biochemical measurements.

For saline-alkaline stress experiments, soil was treated with 150 $mmol \cdot L^{-1}$ NaCl or 150 $mmol \cdot L^{-1}$ $NaHCO_3$ solution after seedling establishment. Seed sterilization, germination, watering (bacterial suspension), and planting procedures were consistent with growth-promoting experiments. Stress treatments are detailed in .

Physiological and Biochemical Measurements

Wheat plants were carefully excavated, soil removed, washed with tap water, and dried. Fresh weight was measured using an analytical balance, plant height and root length measured with a precision ruler, and dry weight determined after oven-drying at 80°C. Chlorophyll content was extracted with ethanol and measured spectrophotometrically. Malondialdehyde (MDA) content was determined by the thiobarbituric acid method. Peroxidase (POD) and catalase (CAT) activities were measured using assay kits (Solarbio Science & Technology, Beijing). Proline content was determined by the sulfosalicylic acid method.

Data Processing and Statistical Analysis

Data were recorded and statistically analyzed using Excel 2019 and SPSS v26.0. One-way analysis of variance (ANOVA) was performed, with values expressed as mean ± standard deviation. Significant differences ($P < 0.05$) are indicated by different letters in tables.

Results

Community Composition of Endophytic Microorganisms in *H. ammodendron* Seeds

High-quality sequencing data were uploaded to NCBI (bacteria: PRJNA1202999; fungi: PRJNA1204448). Four replicate samples yielded 1,647,450 high-quality sequences (>97% similarity) for bacteria, with each sample producing at least 40,918 clean reads. For fungi, 590,844 high-quality sequences were obtained, with each sample producing at least 46,270 reads. Shannon curves plateaued with increasing read numbers, indicating sufficient sequencing depth to reflect bacterial community structure.

At the phylum level ([Figure 2: see original paper]), endophytic bacteria were dominated by Firmicutes (53.85%) and Bacteroidetes, along with Proteobacteria, Desulfobacterota, Campylobacterota, Actinobacteriota, and Patescibacteria. Endophytic fungi ([Figure 2: see original paper]) were dominated by Ascomycota and Basidiomycota, with additional phyla including Mortierellomycota, Rozellomycota, Mucoromycota, Chytridiomycota, Glomeromycota, and Monoblepharomycota.

At the genus level ([Figure 3: see original paper]), endophytic bacteria included *Lachnospiraceae_{{{NK4A136}}*{{group}}}*, unclassified *Muribaculaceae*, *Alistipes*, unclassified *Lachnospiraceae*, unclassified *Desulfovibrionaceae*, *Helicobacter*, and *Prevotella*. The dominant genera were *Lachnospiraceae*{{{NK4A136}}_{{group}}}* and unclassified Bacteroidetes, each exceeding 30% relative abundance. Endophytic fungi comprised unclassified fungi, unclassified Ascomycota, *Aspergillus*, *Cladosporium*, *Fusarium*, *Penicillium*, *Mortierella*, *Thermomyces*, and *Candida*, with unclassified fungi and unclassified Ascomycota as dominant genera (>10% relative abundance each).

Alpha Diversity of Endophytic Microbial Communities

Alpha diversity indices including Chao1, Simpson, Shannon, and Coverage were calculated (). High coverage values (>98%) indicated sufficient sampling depth. Bacterial communities exhibited higher Chao1 richness (1,647.45 ± 29.79) and Shannon diversity (7.78 ± 0.02) compared to fungal communities (Chao1: 593.11 ± 126.47; Shannon: 7.36 ± 0.19), indicating greater bacterial abundance and diversity.

Functional Annotation of Endophytic Microbial Communities

Functional prediction using FAPROTAX revealed that endophytic bacteria were primarily enriched in chemoheterotrophy (36.10%), fermentation (30.88%), sulfate respiration, and animal parasites or symbionts ([Figure 4: see original paper]). Notably, human gut, animal gut, and pathogenic functions were also detected, suggesting potential pathogenic bacteria alongside beneficial microbes. FUNGuild analysis of fungal communities showed predominant functions including undefined saprotrophs (33.61%), wood saprotrophs (13.50%), fungal parasites (12.56%), plant pathogens, dung saprotrophs, animal endosymbionts, and ectomycorrhizal fungi ([Figure 4: see original paper]).

Isolation and Identification of Endophytic Bacteria

A total of 13 endophytic bacterial strains (HB-1 to HB-13) were isolated, belonging to *Bacillus*, *Priestia*, *Kocuria*, *Peribacillus*, and *Terribacillus* (). *Bacillus* was the dominant genus (53.85%, 7 strains), including *B. altitudinis*, *B. pumilus*, *B. aerius*, *B. zhangzhouensis*, *B. safensis*, *B. licheniformis*, and *B. pumilus* HB-11. *Priestia* comprised 2 strains: *P. aryabhattai* HB-4 and *P. megaterium* HB-9.

Kocuria included *K. rosea*, *Peribacillus* included *P. frigoritolerans*, and *Terribacillus* included *T. aidingensis*. All sequences were deposited in GenBank.

Plant Growth-Promoting Properties of Isolated Strains

Functional screening revealed that among the 13 strains, 7 produced IAA, 5 fixed nitrogen, 7 solubilized phosphorus, and 6 produced siderophores (). Five strains exhibited saline-alkaline tolerance. *P. aryabhattai* HB-4 showed the highest IAA production (18.48 ± 2.70 $g \cdot mL^{-1}$), significantly higher than other strains. *P. megaterium* HB-9 demonstrated the strongest phosphorus solubilization ability. *B. zhangzhouensis* HB-6 and *B. pumilus* HB-11 possessed both nitrogen fixation and phosphorus solubilization capabilities. *P. megaterium* HB-9 exhibited combined IAA production, phosphorus solubilization, and siderophore production.

Pot Experiment Results

Strains HB-4 and HB-9 significantly improved wheat physiological indices compared to the control (). HB-4 increased fresh weight, dry weight, and stem length by 125.00%, 75.00%, and 29.18%, respectively, while enhancing chlorophyll content by 43.75% and reducing MDA content by 42.13%. HB-9 promoted root growth and antioxidant enzyme activity, increasing root length by 45.31% and POD activity by 120.33%. These results indicate both strains effectively promote wheat growth, with HB-4 showing advantages in photosynthesis and osmotic regulation, and HB-9 excelling in root development and antioxidant activity.

Under salt stress (), wheat growth was significantly inhibited, but inoculation with *B. zhangzhouensis* HB-10 and *B. pumilus* HB-11 alleviated this inhibition. HB-10 increased fresh weight, dry weight, and stem length by 26.47%, 27.78%, and 29.20%, respectively, while enhancing chlorophyll content by 27.78% and reducing MDA content by 33.65%. HB-11 showed even stronger effects, increasing fresh weight and root length by 36.02% and 26.33%, respectively, and elevating CAT and POD activities by 165.10% and 69.19%. Under alkaline stress (), HB-10 and HB-11 also demonstrated significant protective effects, increasing biomass, enhancing photosynthetic pigments, activating antioxidant systems, and promoting proline accumulation. Both strains effectively mitigated oxidative damage (MDA reduction of 36.59%-73.88%) and enhanced stress resistance, with HB-11 showing superior performance under alkaline conditions.

Discussion

This study systematically analyzed the community composition and ecological interactions of seed endophytic microorganisms in *H. ammodendron* from arid habitats, combining high-throughput sequencing with traditional culture methods. Theoretically, two breakthrough findings were revealed. First, *H.*

ammodendron seed endophytic microorganisms exhibit a unique "dual-engine" pattern: endophytic bacteria are dominated by Firmicutes and Bacteroidetes, with chemoheterotrophy (36.10%) and fermentation (30.88%) as core metabolic modules. Functional gene enrichment analysis showed that nitrogen metabolism-related genes (*narG*, *nifH*) were higher than in non-extreme environment plants like *Eucommia ulmoides*, suggesting this metabolic bias may be closely associated with the host' s evolutionary strategy for adapting to low-nitrogen stress in deserts. Second, the fungal community' s degradation functional group, composed of undefined saprotrophs (33.61%) and wood saprotrophs, may synergistically participate in seed coat lignin decomposition through cellulase secretion, providing microbial evidence for explaining the physiological mechanism of rapid physical dormancy release in *H. ammodendron* seeds under drought conditions. These findings expand the applicability boundaries of "plant-microbe" symbiosis theory in extreme environments and suggest that vertical transmission of seed endophytic microbiomes may be an important carrier for intergenerational adaptation in desert plants—a hypothesis previously reported in rice seed microbiomes.

From an applied perspective, this study successfully constructed a resource library of *H. ammodendron* seed endophytic microorganisms comprising 13 strains (53.85% *Bacillus*). *Priestia* strains HB-4 and HB-9 exhibited multi-target growth-promoting characteristics, while *Bacillus* strains HB-10 and HB-11 demonstrated dual-dimension stress resistance. In cross-species experiments, these strains showed functional plasticity. For instance, *P. megaterium* promoted *Arabidopsis* growth under iron deficiency, while *B. safensis* helped radish and oat resist salt stress, increasing crop yields. This broad-spectrum growth-promoting effect suggests desert plant seed endophytic microorganisms may have functional potential beyond host restrictions, providing theoretical support for developing "modular microbial agents" applicable to multiple crops by integrating stress-resistance genes from *H. ammodendron* strains with host-adaptability genes from crop-associated strains.

However, this study has important limitations regarding host specificity. Although strains showed significant growth-promoting and stress-resistance functions in the "wheat-microbe" system, functional variation may occur in cross-species applications, potentially related to differences in root exudates and soil microbial enrichment among crops. Multi-strain synergistic effects offer an effective solution. For example, *Bacillus subtilis* and *Trichoderma harzianum* synergistically suppress potato common scab, while rice seed endophytic microbiomes collectively promote seed germination. These findings emphasize the need to establish "strain-crop adaptability" evaluation and strain combination systems when promoting microbial applications, using metabolomics to further elucidate regulatory networks between root exudates and strain functional expression.

Conclusion

This study combined high-throughput sequencing and plate isolation techniques to demonstrate that *H. ammodendron* seeds harbor abundant endophytic microorganisms with diverse functions. A total of 13 culturable endophytic bacterial strains were isolated. *P. aryabhattai* HB-4 and *P. megaterium* HB-9 showed excellent growth-promoting effects on wheat seedlings, while salt-alkaline tolerant strains *B. zhangzhouensis* HB-6, *B. safensis* HB-10, and *B. pumilus* HB-11 alleviated stress damage in wheat. Inoculation with HB-10 and HB-11 significantly enhanced biomass, stem length, root length, photosynthesis, and antioxidant enzyme activity. Saline-alkaline stress severely inhibited wheat growth, but strains HB-10 and HB-11 effectively alleviated this inhibition through differential physiological regulation pathways. This may imply synergistic evolution of "plant-microbe" interactions under saline-alkaline stress. Future research should further explore the growth-promoting mechanisms of these strains and develop them for practical applications. This study provides a reference for functional studies and biocontrol applications of *H. ammodendron* seed endophytic bacteria.

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