Effects of different growth patterns of *Tamarix chinensis* on saline-alkali soil: implications for coastal restoration and management

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Abstract

**Objective** To better understand the wetland restoration, the physicochemical property and microbial community in rhizosphere and bulk soil of the living and death *Tamarix chinensis* covered soil zones were studied.

**Results** There were differences between growth conditions in the levels of soil pH, salinity, SOM, and nutrient. The living status of *T. chinensis* exhibited higher capacity of decreasing saline-alkali soil than the death condition of plants, and the living *T. chinensis* showed higher uptake of N, P, and K as compared with the death samples. *Proteobacteria, Bacteroidota*, and *Chloroflexi* were the predominant bacterial communities as revealed via high-throughput sequencing.

**Conclusions** It is great potential for using halophytes such as *T. chinensis* to ecological restore the coastal saline-alkali soil. This study could contribute to a better understanding of halophyte growth during the coastal phytoremediation process, and guide theoretically for management of *T. chinensis* population.

**Keywords** Coastal saline-alkali soil · Phytoremediation · Root-associated microbiome · Soil property · *Tamarix chinensis*

Introduction

Wetlands are one of the most fragile, productive, and valuable natural ecosystems. Saltmarshes are major components of coastal habitats. However, they have experienced a rapid decline globally mainly through human-induced disturbances and natural stressors (Li et al. 2019). A recent report from Chen et al. (2022) showed that the distribution of 7 major species in saltmarshes in the intertidal zone of China had declined from 151,324 ha in 1985 to 115,397 ha in 2019. Indeed, high soil salinity is the primary limiting factor influencing plant growth. Halophytic plants are one of the typical vegetation types in coastal ecosystem. They can tolerate high salinity due to their different exclusion, compartmentation, and excretion resistance mechanisms (Rathore et al. 2017). *Tamarix chinensis* Lour. is one of the salt-tolerant shrub species that is widely distributed in coastal habitats worldwide (Feng et al. 2018). This species is found in the western USA, where it is considered as an
invasive species (Swaminathan et al. 2020; Xie et al. 2020). In China, *T. chinensis* is the vital part of the coastal wetland ecological restoration projects of “Southern Mangrove and Northern Tamarisk” and “Blue Carbon” (Xie et al. 2019; Yang et al. 2021). As one of the dominant shrub in northern China, *T. chinensis* contributes largely to shoreline protection, carbon sequestration, and ecological function (Jiao et al. 2021; Xie et al. 2020). Moreover, this species is often used for saline soil rehabilitation in China due to its strong salt tolerance, drought, and flooding (Chen et al. 2019; Feng et al. 2018).

In response to the degradation of coastal ecosystems worldwide, there has triggered growing interest in developing techniques for the restoration of degraded coastal habitats. In China, the coastal restoration projects have multiplied in recent years, with more than 1 billion US dollars spent during the period of 2016 to 2019 (Liu et al. 2021). As an eco-friendly and cost-effective technology, phytoremediation is a promising way to improve the damaged wetland ecosystems and ameliorate saline soil (Zhou et al. 2020). A previous study found that the establishment of halophytes on saline soil could change the soil properties (Feng et al. 2018). Jing et al. (2019) pointed out that halophytes could assist in coastal soil desalination, altered soil properties, enzyme activities. Furthermore, halophytes are capable of restoring coastal wetlands by absorbing excess nutrients and pollutants (Jiang et al. 2015). Therefore, it is great potential for using halophytes to restore the coastal saline-alkali soil.

Microorganisms are abundant and diverse in soils. Microbes play significant roles in the biogeochemical cycle and ecological function of wetlands (Li et al. 2021). It has been reported that the distinct patterns of growth of halophytes could result in differential communities and degrees of microbial activities in root associated soil (Rathore et al. 2017). Rhizosphere is a habitat in which microorganisms are directly influenced by plant roots (Chaudhary et al. 2018). The rhizosphere receives continuously input from the exudation of plant roots, which contribute to the rhizosphere a carbon-rich environment for the enrichment of microbial communities (Sasse et al. 2018). Zhang et al. (2011) emphasized that rhizosphere microbial processes are vital factors in determining the survival and sustainable growth of plant. Although many studies have focused on environmental variations on soil properties, and little attention has been paid to the difference of microbial community in the rhizosphere and non-rhizosphere soil between living and death (i.e., gradually died) halophytes after the establishment of vegetation. To the best of our knowledge, no study has been carried out yet to study the rhizosphere and bulk soil bacteria presented in the roots associated soils of different growth status of *T. chinensis*. Comparing the root-associated microbes between different growth patterns of plants is crucial for understanding plant–microbe interactions during bioremediation mechanism.

A restored coastal tidal flat site located on the Zhoushan island was chosen in this study. After 2 years of vegetation, the majority of *T. chinensis* had strong salinity adaptability in this region. However, a minority of this species gradually died. To effectively protect and restore saltmarshes, a deep understanding of plant growth pattern is necessary. Here, we hypothesized that the variations of root-associated bacteria were likely attributed to the changes of physicochemical property of living and death *T. chinensis*-covered soils. High-throughput sequencing technique was used to analyse the variations in the soil property and the diversity and composition of bacteria in different compartments (rhizosphere and bulk soil) from two status of living and death *T. chinensis* wetlands.

**Material and methods**

**Site description**

Sampling sites were located in a coastal ecological restoration project site in Dinghai district (29° 32’-30° 04’ N, 121° 30’-123° 25’ E), Zhoushan island, Zhejiang Province (Fig. 1). It has a subtropical monsoon climate with an annual average temperature of approximately 16 °C, and the annual average sunshine duration is 1941–2257 h (Lin et al. 2018). The coastline type of the study area is mainly composed of tidal flat wetlands. The replacement of invasive *S. alterniflora* with several local plant species in the mean high tide level was completed in December 2019 for coastal flat restoration, including *Suaeda australis, Phragmites australis*, and *Tamarix chinensis*. The living *T. chinensis*-covered zone and death zone of rhizosphere and bulk soils were collected in this study. The living and death of *T. chinensis*-covered
rhizosphere soil samples were named as TLR and TDR, while the living and death of T. chinensis-covered bulk soils were named as TLB and TDB. The bare mudflat without plants was termed as MUD.

Soil collection and analysis

Soil samples were collected in triplicates in January 2022. The roots of T. chinensis of living and death status were separately shaken vigorously to separate soil not tightly adhering to the roots (i.e., bulk soil) and attached to roots (i.e., rhizosphere soil). All visible plant residues, litter materials, macrofauna, and stone pieces were removed, and the soil samples were placed separately into aseptic bags and then brought back to the laboratory immediately. Bulk soil sample was divided into two parts. One part of bulk soil and MUD were used to determine the soil physical-chemical properties; the other set of bulk soil and the rhizosphere soil were maintained at – 80 °C before high throughput sequencing analyses.

Soil pH in each sample was detected using a digital pH meter. Soil salinity was determined after drying residue method. Soil moisture content was analysed by the weight loss of the soil after drying at 105 °C until weight stability. Soil organic matter (SOM) was measured using the dichromate titration method. Total nitrogen (TN), available nitrogen (AN), total phosphorous (TP), and available phosphorous (AP) were determined by standard methods (Zhang et al. 2019). Soil total potassium (STK) and available potassium (SAK) were measured using graphite furnace atomic absorption spectrometry.

Soil DNA extraction and high throughput sequencing

The total genomic DNA was extracted from ~0.5 g of the samples using the Soil DNA Kit (D5625, OMEGA) following the manufacturer’s protocols. The concentration and purity of the DNA were quantified by Qubit®3.0 (Life Invitrogen). The integrity of the DNA was verified by running electrophoresis on 2% agarose gel. The V4–V5 regions of 16S rRNA genes of the samples were then subjected to sequencing. The 16S rRNA genes were amplified using the primers 515F (5′-GTG CCA GCMGCC GCG G-3′) and 907R (5′-CCG TCA ATTCMTTT RAG TTT-3′) by PCR (95 °C for 5 min, followed by 27–30 cycles at 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 45 s and a final extension at 72 °C for 5 min). PCR reactions were performed in 30 μL mixture containing 15 μL of 2 × Phanta Master Mix, 1 μL of each primer (10 μM), and 20 ng of template DNA. Amplicons were extracted from 2% agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, U.S.) according to the manufacturer’s instructions and quantified using Qubit®3.0 (Life Invitrogen). The amplicon library was paired-end sequenced (2 × 250) on an Illumina Novaseq 6000 platform (Nanjing GenePioneer Co. Ltd) according to the standard protocols. The PCR chimeras were detected and filtered out using the Vsearch uchime-denovo algorithm. The PE reads were overlapped to assemble the final tag sequences with the minimum overlap length as 10 bp with PAN-DASeq (Masella et al. 2012). Quality filtering of MiSeq reads was carried out by PRINSEQ according to specific filtering conditions to obtain the high-quality clean tags.

Fig. 1 Location of the study area
Analysis of sequencing data

The sequences with ≥97% similarity were assigned to the same operational taxonomic units (OTUs) by Vsearch (Version 2.15.0). The phylogenetic affiliation of each 16S rRNA gene sequence was analyzed by uclust against the silica (SSU132)16S rRNA database using confidence threshold of 90%. The rarefaction analysis based on QIIME (1.9.1) was conducted to reveal the diversity indices (Caporaso et al. 2010). Chao1 index was calculated to compare the diversity of the bacterial communities (Chao 1984). Beta-diversity using both weighted and unweighted UniFrac was calculated by QIIME 1.9.1 (Lozupone et al. 2011). Principal coordinate analysis (PCoA) was conducted using the QIIME 1.9.1 to examine dissimilarities in community composition.

Results and discussion

Soil characterization

It has been reported that plants could alter soil properties via nutrient cycling and litter decomposition (Cao et al. 2014). After 2 years of plantation, the results of soil physicochemical properties are tabulated in Table 1. The pH of MUD was 8.54, the pH of TDB was higher than TLB. Soil salinity was lower in soils under plant-covered sites than in MUD. These results indicated that *Tamarix chinensis* could decrease soil pH and desalinization was occurred, the living status of *T. chinensis* exhibited higher capacity of decreasing saline-alkali soil than the death condition of plants. The SOM of plant-covered soils was obviously higher than MUD, with the highest SOM value in TLB. This result might be related to the litter decomposition and below-ground biomass (Cao et al. 2014; Chaudhary et al. 2015; Shao et al. 2015). A previous study showed that salinity and alkalinity could reduce the SOM accumulation in coastal wetlands (Xie et al. 2017). Wang et al. (2010) also illustrated that the increase in SOM could decrease the accumulation of salinity by improving soil porosity and water permeability. Levels of TN, TP, STK, and SAK were in the following order: MUD > TDB > TLB. These results indicated that the higher uptake of N, P, and K by *T. chinensis* to regulate N and P mineralization, osmotic adjustment (Rathore et al. 2017). Overall, the physicochemical properties of bulk soil were quite different between TLB and TDB.

**Table 1** Soil physicochemical parameters of *Tamarix chinensis* coverage and bare mudflat

|        | TLB   | TDB   | MUD   |
|--------|-------|-------|-------|
| pH     | 7.14  | 8.51  | 8.54  |
| Moisture (%) | 19.8  | 24.2  | 63.3  |
| SOM (g/kg) | 97.3  | 90.1  | 16.6  |
| Salinity (g/kg) | 5.05  | 14.1  | 28.7  |
| TN (mg/kg) | 316   | 350   | 504   |
| AN (mg/kg) | 34.0  | 39.2  | 40.6  |
| TP (mg/kg) | 174   | 484   | 520   |
| AP (mg/kg) | 11.3  | 18.4  | 14.2  |
| STK (%) | 1.01  | 1.49  | 1.62  |
| SAK (mg/kg) | 153   | 416   | 693   |

Bacterial community diversity

Soil microbial diversity is one of the direct indicators of soil health, fertility, and function (Xu et al. 2019). Soil bacterial communities were analysed through high throughput sequencing approach. As shown in Fig. 2, it can be seen that the rarefaction curve reached plateau, suggesting the bacterial diversity covered sufficiently at the sequencing depth. Chao1 richness was analysed to compare the levels of alpha diversity indices in different treatment (Fig. 3). The indices of Chao1 in TDR was markedly higher than TLR, indicating that the bacterial communities in the rhizosphere soil of death status were more diverse. In addition, there were no obvious differences in the bulk soils of the plant species in different conditions. Liu et al. (2016) exhibited the Chao1 index of dense *T. chinensis*-covered bulk soils was 1475 in November and 1607 in September, which is in line with the present study.

The sequence data was subjected to PCoA based on weighted UniFrac distance analysis. As shown in Fig. 4a, the first two PCs explained a total of 41.94% variance of bacterial communities in rhizosphere soils, the bacterial communities were clearly clustered into two groups, the condition of living plant species was separated from those of death treatment. Similarly to the rhizosphere soil communities, the first two PCs explained a total of 41.33% variance of bacterial communities, there was distinct two groups.
clustered between the living and death *T. chinensis*-covered bulk soils (Fig. 4b). These results indicated that the different status of plant species in both rhizosphere and bulk soils could dramatically change the bacterial community diversity.

Predominant bacterial community composition at the phylum level

The composition of the bacterial communities at the phylum level in the bulk soil and the rhizosphere soil from all the samples are presented in Fig. 5. In the rhizosphere soils, the major phyla were *Proteobacteria*, *Bacteroidota*, *Chloroflexi*, *Acidobacteriota*, *Desulfobacterota*, *Planctomycetota*, *Gemmatimonadota*, *Actinobacteriota*, *Myxococcota*, *Latescibacterota*, which accounted for more than 90% of the bacterial sequences obtained from the rhizosphere soils. *Proteobacteria*, *Bacteroidota*, *Chloroflexi* were dominant in the rhizosphere samples. As for bulk soils, the main phyla were *Proteobacteria*, *Bacteroidota*, *Chloroflexi*, *Acidobacteriota*, *Actinobacteriota*, *Gemmatimonadota*, *Planctomycetota*, and *Myxococcota*. Similarly to the rhizosphere soil communities, *Proteobacteria*, *Bacteroidota*, *Chloroflexi* were dominant in bulk soils.

*Proteobacteria* was the major phylum in all the samples, which is consistent with the findings of previous studies on other halophyte covered soils such as *Atriplex triangularis*, *Suaeda glauca*, *Messerschmidia sibirica*, *Salicornia europaea*, and *Phragmites australis* (Jing et al. 2019; Tian and Zhang 2017; Zhang et al. 2019; Zhao et al. 2016). The phylum *Proteobacteria* accounted for the largest proportion across samples might be attributed to its capacity to metabolize various substrates (Eilers et al. 2010; Zhao et al. 2020). Previous report showed that *Bacteroidota* might participate in the decomposition of organic matter (An et al. 2022). Ward et al. (2009) reported

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**Fig. 2** Rarefaction curves of all samples

**Fig. 3** Chaol index of all samples
that Acidobacteria played a vital role in the cycling of organic matter derived from plants. Therefore, the relative abundance of these phyla in the present study might be due to the higher root exudate in the coastal soils of Zhoushan Island. For comparison, higher abundance of Bacteroidota was observed in TLB as compared with TLR, indicating the bacteria in bulk soils had higher capacity of degrading organic matter than that of rhizosphere soils in the healthy ecosystem of T. chinensis. Higher abundance of Acidobacteria was found in TDR and TDB samples compared with TLR and TLB, suggesting the bacteria in death plant soils exhibited higher decomposition of organic matter derived from plants. Besides, Proteobacteria, Chloroflexi, Acidobacteriota are fast growing Gram-negative bacteria, and their carbon sources are simple and easy to use (Yin et al. 2018). It has been reported that Proteobacteria, Chloroflexi, Acidobacteria, and Bacteroidetes were the dominant bacterial phyla in wetlands across China (An et al. 2019). Furthermore, Jing et al. (2019) demonstrated that Proteobacteria, Bacteroidota, Chloroflexi were the dominant bacterial phyla in the rhizosphere and bulk soils of halophytes in the saline coastal wetlands of the Yellow River Delta. However, a study in coastal saline-alkali soil under T. chinensis woodland at Bohai Bay revealed that Proteobacteria, Acidobacteria, and Actinobacteria were the dominant phyla (Liu et al. 2016). It is likely that the soil type, vegetation type, seasonality,
the distance to seashore line might play important role in soil characteristics and shape the composition of the bacterial communities (Liu et al. 2016; Shao et al. 2015). Overall, bacterial community might be used as a bioindicator for coastal ecological restoration project and wetland degradation of T. chinensis.

**Conclusions**

This study revealed the changes in soil properties and bacterial communities in different compartments (bulk soil and rhizosphere soil) of living and death Tamarix chinensis wetlands. T. chinensis could decrease pH and salinity of soil, the living status of T. chinensis exhibited higher capacity of decreasing saline-alkali soil than the death condition of plants. The physicochemical properties of bulk soil obviously differed between TLB and TDB. Lower values of Chao1 were found in living rhizosphere of T. chinensis soils than in death condition, while there were no obvious differences in the bulk soils of the plant species in different conditions. Results showed that the predominant bacterial communities were Proteobacteria, Bacteroidota, and Chloroflexi. This study could contribute to a better understanding of rhizosphere and bulk microbiota in T. chinensis-covered coastal wetland ecosystems.

**Author contributions**  CG, JYS, JLR, YT: conceived and designed the study. WBH, QS, and YMY: conducted the literature search and performed the experiments. ZNL and YC: were involved in the analysis and interpretation of data. YT: drafted the manuscript. XJC, SDD and CHY: The study was supervised and tutored. All authors read and approved the final manuscript.

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**Declarations**

**Conflict of interest**  The authors declare that they have no conflict of interest.

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