Effect of industrial crop Jerusalem artichoke on the micro-ecological rhizosphere environment in saline soil

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Abstract

Salinity is not only a threat to organisms and ecosystems, but also a major factor restricting the development of agricultural production. This study aimed to explore the modification effect of in-situ Jerusalem artichoke (genotype NY-1) cultivation on the rhizosphere micro-ecological environment in the saline-alkali region along the southeast coast of China. We analyzed the change of carbon and nitrogen in the saline soil from a microbial perspective, through the quantification of the area of root channels, rhizosphere secretions and soil microbiome (cbbL, cbbM and nifH). The root channels of NY-1 not only improved the physical structure of saline soil, but also provided a living space for microorganisms, afforded basic conditions for the optimization of the soil micro-ecological environment. In addition, rhizosphere secretions (from roots of NY-1 as well as microorganisms), such as carbohydrates, hydrocarbons, acids, etc., could be considered as a way to improve the saline-alkali soil habitat. NY-1 increased the diversity and abundance of autotrophic and nitrogen-fixing bacteria in saline soil (rhizosphere > bulk soils), which should be a biological way to increase the amount of carbon and nitrogen fixation in soil. Moreover, some of the detected genera (Sideroxydans, Thiobacillus, Sulfuritalea, Desulfuromonas, etc.) participate in the carbon and nitrogen cycles, and in the biogeochemical cycle of other elements. In short, Jerusalem artichoke can improve not only the physical and chemical properties of saline-alkali soil, but also promote material circulation and energy flow in the micro-ecological rhizosphere environment of saline soils.

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Abstract

Salinity is not only a threat to organisms and ecosystems, but also a major factor restricting the development of agricultural production. This study aimed to explore the modification effect of in-situ Jerusalem artichoke

(genotype NY-1) cultivation on the rhizosphere micro-ecological environment in the saline-alkali region along the southeast coast of China. We analyzed the change of carbon and nitrogen in the saline soil from a microbial perspective, through the quantification of the area of root channels, rhizosphere secretions and soil microbiome (*cbbL, cbbM* and *nifH*). The root channels of NY-1 not only improved the physical structure of saline soil, but also provided a living space for microorganisms, afforded basic conditions for the optimization of the soil micro-ecological environment. In addition, rhizosphere secretions (from roots of NY-1 as well as microorganisms), such as carbohydrates, hydrocarbons, acids, etc., could be considered as a way to improve the saline-alkali soil habitat. NY-1 increased the diversity and abundance of autotrophic and nitrogen-fixing bacteria in saline soil (rhizosphere > bulk soils), which should be a biological way to increase the amount of carbon and nitrogen fixation in soil. Moreover, some of the detected genera (*Sideroxydans, Thiobacillus, Sulfuritalea, Desulfuromonas*, etc.) participate in the carbon and nitrogen cycles, and in the biogeochemical cycle of other elements. In short, Jerusalem artichoke can improve not only the physical and chemical properties of saline-alkali soil, but also promote material circulation and energy flow in the micro-ecological rhizosphere environment of saline soils.

Keywords

In-situ, microbial community, nitrogen fixation, secretions, root channel

1. Introduction

Due to global climate change and increasing population pressure, 33% of global soil is moderately to highly degraded through erosion, salinization, compaction, acidification, chemical pollution, and nutrient depletion, hampering soil functions and affecting food production (Abogadallah, 2010; Mao et al., 2016). Soil salinization causes damage not only to natural resources, but is also a major factor restricting the development of agricultural production and improving land-use efficiency, and is also a threat to organisms and ecosystems (Liu et al., 2018; Yu, Liu, Yang, Fan & Zhou, 2018; Xia, Ren, Zhang, Wang & Fang, 2019). Nevertheless, saline soils are widely distributed on the earth surface, covering approximately 7-8% of the world land area, making them a potentially important land resource (Shrivastava & Kumar, 2015; Jiang et al., 2019).

In saline soils, salinity as well as alkalinity damage plant roots very seriously. Roots play an important role in plant growth. Roots extract nutrients and water from soil, and also exude a variety of organic and inorganic compounds into the rhizosphere soil. These exuded compounds change the chemistry and biology of the rhizosphere soil, making it significantly different from the bulk soil further away from roots (Marschner, 1995; Zhang, Li, & Wang, 2007). Plants form a specific bacterial community structure in the rhizosphere soil through specific root exudation, and the secondary metabolites produced by some rhizosphere bacteria can promote plant growth (Sturz & Christie, 2003). Furthermore, soil microbes also play an important role in maintaining the stability of ecosystems; they reflect the evolution of soil quality and are one of the indicators of the ecosystem health (Diacono & Montemurro, 2010).

Jerusalem artichoke (*Helianthus tuberosus* L.), which belongs to the Asteraceae family, is a tuber-forming perennial distributed worldwide (Shi et al., 2011). Jerusalem artichoke is an excellent crop because it has strong resistance to abiotic stresses (drought, salinity, etc.), high photosynthetic efficiency, low fertilizer and water demand, great ecological restoration capacity, and high commercial value. It is easily grown in saline and alkaline soils, and it can also be used for soil and water conservation and fixing terraces and unstable sand (Long et al., 2010; Shao et al., 2019).

In this paper, we aimed to explore an *in situ* remediation technology using Jerusalem artichoke to improve the micro-ecological environment of saline soils varying in salinity in the southeast China. Through the quantification of the area of root channels, rhizosphere secretions and soil microbiome, the change of carbon and nitrogen in the saline soil was analyzed, and the modifying effect of Jerusalem artichoke cultivation on the micro-ecological rhizosphere environment in saline soil was elucidated.

2. Materials and methods

2.1 Location and materials

The experimental field was located at Dafeng port (33°14' N, 120deg 44' E), Dafeng district, Yancheng city, on the east coast of Jiangsu province.

The naturally saline experimental field (pH 7.13-8.16) was divided based on different salt content (g salt kg^{-1} soil) into high salinity (H, 4.1-5.0), moderate salinity (M, 2.9-3.9) and low salinity (L, 1.5-2.0). Different salinity levels had the same initial soil properties, and the soil (silty clay loam) was contained 65% silt and 18% clay.

The grass was mowed before plowing using a conventional moldboard plow. We selected *Helianthus tuberosus* L. cv. NY-1 (Su-Jian Jerusalem artichoke 200901) as a test material. NY-1 was planted with 0.6 m row spacing and 0.4 m intra-row spacing. No fertilizer and no irrigation was used during the 8-year period. Five replicate plots (5 x 5 m each) were planted in each area (Shao et al., 2019).

Soil was sampled in each replicate plot as follows: control soil (no Jerusalem artichoke planting, no human influence), rhizosphere soil (attached to the root system of Jerusalem artichoke) and bulk soil (away from Jerusalem artichoke roots). One composite sample (containing five soil cores) was taken from each replicate plot by the five-point sampling method (depth of 0-20 cm) using a soil auger (6 cm diameter). All soil samples were packaged in separate sterile plastic bags; a portion of each soil sample was wrapped in tin foil, labeled, and snap-frozen in liquid nitrogen for subsequent DNA extraction and molecular analysis. The remaining soil was air-dried and passed through a 0.15-mm sievs, then stored in a refrigerator at 4 for soil biological and chemical analyses (Lauber, Zhou, Gordon, Knight & Fierer, 2010; Tatangelo, Franzetti, Gandolfi, Bestetti & Ambrosini, 2014).

In addition, undisturbed soil columns were collected for the determination of root channels below the plants as well as in the inter-row positions. The sampling tools were rigid PVC pipes (inner diameter of 11 cm, length of 40 cm, wall thickness of 0.2 cm) with a sharp edge at one end for driving into the soil profile. The extracted soil columns were wrapped in plastic for transport to the lab.

2.2 Methods (See Appendix 1)

2.2.1 Root channels

The area of root channels was characterized using a 64-row multi-slice spiral computed tomography CT scanner (Light Speed VCT, Jiangsu Provincial Hospital of Integrated Traditional Chinese and Western Medicine) (San, Caniego & Garcia, 2017). The images (Figure A.1) were processed by running the "Intelligent Identification System for Pores in Saline Soil" V1.0 (2018SR074781). The minimum pixel area was set as 1, ie. the minimum identified root channel diameter was 0.298 mm.

2.2.2 Rhizosphere secretions

We used ethyl acetate to extract the rhizosphere soil secretions and then profiled them using gas chromatography-mass spectrometry (GC-MS) (TSQ 8000TM Evo Triple quadrupole GC-MS, Thermo Fisher Scientific Co., Ltd., Shanghai, China) (Carvalhais et al., 2015; Liu et al., 2015).

2.2.3 Illumina sequencing

Specific primers with the barcode or fusion primers with dislocation of the bases were synthesized according to the designated sequencing regions. The primers for *cbbL* , *cbbM* and *nifH* were 595F/1387R, 490F/974R and PolF/PolR, respectively. A TransGen AP221-02: TransStart FastPfu DNA polymerase 20 μL reaction system was used (Alfreider, Vogt, Hoffmann & Babel 2003; Tourova, Kovaleva, Sorokin & Muyzer, 2010; Shao et al., 2019; Xu et al., 2020; Yue et al., 2020).

Data availability: The complete sequencing data sets have been deposited in the NCBI Sequence Read Archive (SRA) database under the accession number PRJNA555455.

2.2.4 Statistical analysis and figure drawing

Statistical analyzes were performed using Microsoft Excel 2007, SPSS Statistics 20.0 (IBM, Armonk, New York, USA) and R package vegan (version 2.5-5). Adobe Illustrator CC 2017 and R package ggplot2 (version 3.2.0) were used to draw figures (Oksanen et al., 2019; Kraemer, Ramachandran, Colatriano, Lovejoy & Walsh, 2020).

The average value of all parameters was taken from the five replicates and the standard error was calculated. The data were analyzed by the multiple t -test (p[?]0.05). Correlation analysis used the Mantel test and Spearman's rank correlation coefficients (Guillot & Rousset, 2013; Sedgwick, 2014). LDA Effect Size analysis (LEfSe) used the ANOVA and then the Wilcoxon rank sum test to analyze the differences between groups (threshold set to 0.05) (Kuffner et al. 2012; Yue et al., 2020).

3. Results

3.1 Root channels

The channel area in each type of soil was larger at a depth of 25 mm than in deeper layers (Figure 1A). At the depth of more than 225 mm, the channel area was small, and there was no significant difference among various types of soil.

In the 0-200 mm and 200-400 mm soil layers, the channel area below the plants grown in the medium (M-UP) and low salinity soil (L-UP) was significantly larger than in the other types of soil (p[?]0.05) (Figure 1B). In soils with low and medium salinity, the difference in root channel area between soil under the plants and the inter-row soil was significant. However, in highly saline soils, the root channel area was similar between the soil under the plants (H-UP) and the inter-row soil (H-IR). In this study, the lowest ratio of the total channel area in 0-200 mm vs. 200-400 mm soil layer was in the inter-row on highly saline soil (H-IR, 4:3). A general trend of channel area in different soils at various soil depths was soil under the plants > inter-row soil, as well as moderate and low salinity soil > high salinity soil (Figure 1B).

3.2 Rhizosphere secretions

The rhizosphere secretions detected in this study could be divided roughly into 15 types: hydrocarbons, acids/esters, alcohols, amines, ketones, nitriles, ammonium salts, aromatic hydrocarbons, hydrazines, amides, sulfonyls, oxides, ethers, aldehydes, and carbohydrates; however, the last seven types were detected only in the low salinity rhizosphere soils (L-R). Acids/esters were found in all soil samples and accounted for a relatively high proportion (43-83%), except in the L-NR (30%) and H-R soils (16%). The other rhizosphere secretions widely present in all soil samples were hydrocarbons, but in a modest proportion, ranging from 1.07% to 9.6% (Figure 2A).

Alcohols were not detected in H-NR, and their relative proportion in the bulk soil was between 4.9% and 7.6%, higher than in the rhizosphere soil (0.24% to 3.2%). Amines were not detected in L-R, the two sample types with the highest relative proportions were L-NR (21%) and H-NR (13%), whereas CK soil had the lowest proportion (0.39%). The relative proportion of ketones in CK was 22%, which was significantly higher than in M-NR, L-NR and H-R (2.9%, 0.24% and 3.4%, respectively). Nitriles were detected only in highly saline soil, with relative proportions of 0.83% in H-NR and 0.19% in H-R (Figure 2A).

The six abundantly detected rhizosphere secretions were acids/esters, ammonium salts, amines, ketones, hydrocarbons, and alcohols (Figure 2A-D). For acids/esters in the bulk soil, the relative proportion increased with an increase in soil salinity, whereas it was mostly opposite in the rhizosphere soil. The relative proportion of ketones in CK soil (22%) was significantly higher than in the other soil types, while amines was significantly higher in L-NR than in the other soil sample types. The relative proportion of alcohols in CK (7.6%) was significantly higher than in the other soil sample types, and it was higher in the bulk soil than the rhizosphere soil (at medium and low salinity).

3.3 Autotrophic and nitrogen-fixing bacteria

Based on the Chao1 and the Shannon index, the community diversity of autotrophic bacteria containing *cbbL* showed the order of bulk soil > rhizosphere soil as well as of high salinity soil > moderate salinity soil =

low salinity soil, and the community richness showed similar orders (Figure 3A). In the diversity information analysis, a total of 8 phyla, 11 classes, 28 orders, 32 families, and 59 genera of autotrophic bacteria containing *cbbL*were detected, of which the 10 dominant genera were*g_Halorhodospira, g_Marichromatium, g_Thioalkalivibrio, g_unidentified, g_Alkalilimnicola, g_Thiobacillus, g_Rhodovulum, g_Cupriavidus, g_Hydrogenophaga,* and *g_Ectothiorhodospira* . The combined relative abundances of these 10 genera was generally above 90% in all soil samples, with the exception of the CK (58%) and H-NR (83%). The common dominant genera in the bulk soils were*g_Thioalkalivibrio* and *g_Marichromatium* (Figure 3B, E).

In the LEfSe analysis of the autotrophic bacteria containing *cbbL*(Figure 3G), the statistically significant biomarkers were:*o_Chromatiales, o_Rhodospirillales, o_Methylococcales* ,*o_Thermales, o_Burkholderiales* , *o_-Rhizobiales, o_Synechococcales* , *o_Gallionellales* and*o_Rhodobacterales* . (Figure 3G).

The community diversity of autotrophic bacteria containing *cbbM*showed the order of rhizosphere soil > bulk soil, which was the opposite of autotrophic bacteria containing *cbbL*(r<-0.6) (Figure 3C, 5). The total of 29 phyla, 47 classes, 94 orders, 138 families, and 276 genera of autotrophic bacteria containing*cbbM* were detected, with the 10 dominant genera being*unidentified, g_Halothiobacillus, g_Sideroxydans, g_Rhodopseudomonas, g_Thiobacillus, g_Sulfuritalea, g_Leptothrix, g_Magnetospirillum, g_Thiohalomonas,* and *g_Thiocystis;* the sum of the relative abundance of the above 10 genera was around 80% in all soil samples. Dominant genera were *g_Halothiobacillus, g_Sideroxydans, g_Rhodopseudomonas* , and *g_Lepthrix* in the rhizosphere soil, whereas *g_Halothiobacillus, g_Thiobacillus, g_Sulfuritalea* , and *g_Thiohalomonas* predominated in the bulk soil. In addition, the abundance of *g_Thiohororhabdus* was lower in the rhizosphere soil (0.44%) than the bulk soil (4.78%) (Figure 3D, F).

In the LEfSe analysis of the autotrophic bacteria containing *cbbM*(Figure 3H), the statistically significant biomarkers were:*o_Nitrospirales, o_Thermales, o_Halobacteriales, o_Chlorobiales, o_Acidithiobacillales, o_-Thiotrichales, o_Chromatiales, o_Rhodospirillales, o_Methylococcales, o_Burkholderiales, o_Desulfovibrionales* , and*o_Pseudonocardiales* .

The community diversity of nitrogen-fixing bacteria containing *nifH* showed the order of rhizosphere soil > bulk soil, which was the opposite of the autotrophic bacteria containing *cbbL* (r<-0.6) and similar to the autotrophic bacteria containing *cbbM* (r>0.6) (Figure 4A, 5). Total of 26 phyla, 52 classes, 100 orders, 163 families, and 309 genera containing *nifH* were detected, with the 10 dominant genera being *unidentified, g_-Desulfuromonas, g_Geobacter, g_Bradyrhizobium, g_Azoarcus, g_Desulfovibrio, g_Geoalkalibacter, g_Azospirillum, g_Anaeromyxobacter,* and *g_Sinorhizobium* . The relative abundances of these 10 genera were between 61% and 69% in the rhizosphere soil and 71%-76% in the bulk soil and CK. The dominant genera in CK and bulk were *g_Desulfuromonas, g_Geoalkalibacter, g_Anaeromyxobacter, g_Pelobacter, g_Desulfobulbus, g_-Pseudomonas, g_Ectothiorhodospira, g_Methylomonas,* and *g_Halorhodospira* , whereas the dominat ones in the rhizosphere soil were*g_Geobacter, g_Desulfovibrio, g_Azospirillum, g_Sinorhizobium, g_Pseudacidovorax, g_Nostoc, g_Dechloromonas, g_Paraburkholderia, g_Rubrivivax,* and *g_Skermanella* (Figure 4B, C).

A variety of unique nitrogen-fixing bacteria containing *nifH* in CK were showed in the LEfSe analysis (Figure 4D) to be statistically significant biomarkers:*o_Chromatiales, o_Burkholderiales, o_Bacteroidetes, o_Rhizobiales, o_Oceanospirillales, o_Desulfobacterales, o_Xanthomonadales, o_Enterobacterales* , and

o_Hydrogenophilales.

The data and the characteristics of important microorganisms are included in Table 1. Furthermore, there was a significant positive correlation between *cbbL* -containing autotrophic bacteria and amines (p[?]0.05), whereas nitrogen-fixing bacteria and*cbbM* -containing autotrophic bacteria each had highly significant negative correlations with nitriles (p[?]0.05) (Figure 5).

4. Discussion

4.1 Root channels

Soil porosity is a *sine qua non* of soil, and root channels are an important part of soil macropores in the

soil system. Root distribution of Jerusalem artichoke was influenced by soil salt content, water content, pH, and other factors (Hartle, Fernandez & Nowak, 2006). In the present study, the root system of Jerusalem artichoke had the best growth under moderate salt stress. Jerusalem artichoke avoided salt damage by not extending roots to deep soil, so most of the root system of NY-1 mainly grew in the soil layer 75-175 mm deep. Hence, the root distribution pattern reflected the adaptive mechanisms of Jerusalem artichoke under salinity stress. Root channels represent a complex interface that is not only the living space of plant roots, microbes and soil animals, but also plays an important role in dynamics of water, nutrients, gas, heat, and other factors in soil (Gupta et al., 2008; Gupta, Naushad & Baker, 2015; Wang, Zhang, Yang, Li & Liu, 2018). The root channels of Jerusalem artichoke improved the physical structure of saline soil and provided basic conditions for the optimization of the soil micro-ecological environment.

4.2 Rhizosphere secretions

Rhizosphere secretions are important in the organic and inorganic matter cycling and energy flow between plants and the environment. Organisms such as plants and microbes adapt to their habitats and influence their surroundings by releasing various high- and low-molecular-weight metabolites and ions into the environment, with up to 50% of photosynthetic products potentially released as rhizosphere secretions (Zhang, Li & Wang, 2007; van Dam & Bouwmeester, 2016). High-molecular-weight metabolites in secretions (carbohydrates, hydrocarbons, etc.) may adhere strongly to soil particles. Such adhesion promotes the formation of soil aggregates, changes the soil structure, and improves the physical and chemical properties of the soil. In addition, organic acid anions could increase availability of nutrients in the rhizosphere by their chelating capacity (Killham, 1994). The acid/ester compounds detected in the present study were mainly dibutyl phthalate (DBP), which is a potential allelopathic substance. Low concentration of DBP increased the content of chlorophyll in leaves and the activities of urease and catalase in soil, and enhanced the plant capacity to resist stress, but high concentration had the opposite effect (Keire et al., 2001; Deng et al., 2017).

Different secretions would have differential effects on the surroundings, including an effect on the formation of a specific microbial community in the rhizosphere soil (Sturz & Christie, 2003), and influencing not only the abundance and type of microorganisms, but also growth and metabolism as well as community composition of microorganisms (Haldar & Sengupta, 2015; Ankati & Podile, 2019; Vives-Peri, de Ollas, Gómez-Cadenas & Perez-Clemente, 2020). Obviously, the rhizosphere microbial community structure is the result of a series of complex interactions and feedbacks between the roots, the microbes and the physical and chemical environment of the soil. There are numerous studies demonstrating that plant development influences the composition and function of the soil microbiome (e.g. Rodriguez, Muñera & Peñuela, 2016; Zhalnina et al., 2018; Shao et al., 2020; Xu et al., 2020). The microorganisms that tend to gather near roots, such as*Geobacter, Cupriavidus, Halorhodospira, Marichromatium, Rhodobacter, Rhodovulum, Rubrivivax, Sideroxydans* ,*Pseudacidovorax, Sinorhizobium, Leptothrix* and*Methylocystis,* etc. in the present study (Figs 3, 4) influence the rhizosphere environment and may decompose and transform rhizosphere secretions.

4.3 Soil microbes

Microorganisms are the driving force for nutrient conversion and cycling, having the characteristics of large biomass, complex community composition, diverse metabolic functions, and complex interactive relationships (Bardgett & van der Putten, 2014). They can mediate important metabolic processes in the carbon and nitrogen cycles (Brussaard, de Ruiter & Brown, 2007). Climate change caused by greenhouse gas emissions has long been an important global issue. Therefore, biological mitigation of CO_2 emissions has attracted the attention of many researchers (Mahinpey, Asghari & Mirjafari, 2011; Farrelly, Everard, Fagan & McDonnell, 2013). Aboveground plant parts provide organic carbon sources for roots and soil organisms, thus influencing strongly the underground system. In particular, rhizosphere secretions provide carbon sources and energy for the growth of microorganisms (Stephan Shockey, Moe & Dorn, 2002; van der Wielen, 2006; Selesi, Pattis, Schmid, Kandeler & Hartmann, 2007).

We found in our previous research that Jerusalem artichoke played a significant role in increasing soil microbial populations. We reported greater relative abundance of p_Proteobacteria, p_Bacteroidetes and p_-

Cyanobacteria in the bulk than rhizosphere soil, whereas p_Acidobacteria, p_Chloroflexi and p_Nitrospirae abundance was greater in the rhizosphere than bulk soil (Shao et al. 2019). Here, almost all autotrophic microorganisms and nitrogen-fixing microorganisms belonged to p_Proteobacteria, and its relative abundance in bulk soil was slightly lower than that in rhizosphere soil.

Among *cbbL* -containing autotrophic bacteria, the relative abundance of *c_Ga mmaproteobacteria* exceeded 65% in the bulk and rhizosphere soils, including the five dominant genera: g_*Halorhodospira, g_Marichromatium, g_Thioalkalivibrio, g_Alkalilimnicola,* and *g_Ectothiorhodospira* , all of which grow in oceans or high-salt environments where the pH is neutral to extremely alkaline (Sorokin, Muntyan, Panteleeva & Muyzer, 2012). There were also three dominant genera: *g_Thiobacillus* , *g_Cupriavidus* and*g_Hydrogenophaga* , all belonging to *c_Betaproteobacteria* .

Almost all of the unique *cbbM* -containing autotrophic bacteria in the rhizosphere soils belonged to *c_Betaproteobacteria, c_Alphaproteobacteria* and *c_Actinobacteria* , and the five dominant genera were *g_Halothiobacillus, g_Sideroxydans, g_Rhodopseudomonas, g_Thiobacillus* , and *g_Sulfuritalea* . The previous research data of our team demonstrated that the content of soil organic carbon (12.8 ± 0.79 g/kg) and total nitrogen of the Jerusalem artichoke planting area (0.96 ± 0.21 g/kg) in this experimental area were significantly higher than those of the bare control soil (5.6 ± 0.89 g C/kg and 0.40 ± 0.04 g N/kg) (Li et al., 2018). In the study presented here, the community diversity of *cbbM* -containing autotrophic bacteria and nitrogen-fixing bacteria containing *nifH* showed the order of rhizosphere soil > bulk soil, which indicated that Jerusalem artichoke could enhance soil fixation of carbon and nitrogen by changing the community composition of soil microorganisms.

Soil environments with low CO_2 concentration are beneficial to the growth of autotrophic bacteria containing the*cbbL* gene, whereas the autotrophic bacteria with the *cbbM*gene are relatively abundant at low oxygen and high CO_2concentrations (Videmsek et al., 2009), which was confirmed in the present study. *Sideroxydans* is a Fe-oxidizing bacterium.*Thiobacillus* and *Sulfuritalea* are ammonia-oxidizing bacteria, and both can also provide the available sulfate-sulfur plants can take up. In addition, *Sulfuritalea* also functions in the denitrification process. Some species of *Hydrogenophaga* also have anaerobic nitrate respiration and are denitrifiers (Vandamme & Coenye, 2004; Jazaeri, Akhgar, Sarcheshmehpour & Mohammad, 2016). Four dominant genera containing *nifH* were: *g_Desulfuromonas, g_Geobacter, g_Geoalkalibacter,* and *g_Anaeromyxobacter, all*belonging to *c_Deltaproteobacteria* (Holmes, Nevin & Lovley, 2004; Zavarzina et al., 2006). *Deltaproteobacteria* exhibit considerable anaerobic physiological diversity, including sulfate reduction, iron reduction (*g_Geobacter*), fermentation, and dehalogenation (Nevin, Holmes, Woodard, Covalla & Lovley, 2007). Moreover, rhizobia *(g_Rhizobium, g_Bradyrhizobium, g_Sinorhizobium* , and *g_Azorhizobium)* are symbiotic nitrogen-fixers, and responsible for the major share of global fixation of atmospheric nitrogen, and require low concentration of oxygen (Viprey, Rosenthal, Broughton & Perret, 2000; Lodwig et al., 2003). In the present study, the abundance of *Gammaproteobacteria* and*Deltaproteobacteria* at given soil salinity was higher in the bulk than rhizosphere soil. In contrast, the relative abundance of*Betaproteobacteria* and *Alphaproteobacteria* was significantly higher in the rhizosphere than bulk soil, and the abundance was higher in low-salinity than high-salinity soils (Table 1). Most *Betaproteobacteria* are resistant to low pH and high temperature, and prefer low-oxygen conditions. Both*Betaproteobacteria* and *Gammaproteobacteria* include nitrogen-fixing rhizobia (Moulin, Munive, Dreyfus & Boivin-Masson, 2001; Shiraishi, Matsushita & Hougetsu, 2010; Klann, McHenry, Montelongo & Goffredi, 2016).

We also found other functional microorganisms such as aerobic methane oxidizing bacteria (*g_Methylibium, g_Methylobacter, g_Methylobacterium, etc.*), desulfurization bacteria (*g__Desulfarculus, g_Desulfatibacillum, g_Desulfitobacterium, etc.*), nitrifying bacteria (*g_Nitrobacter, g_Nitrosospira, g_Nitrospira, etc.*), sulfur-oxidizing bacteria (*g_Sulfuricurvum, g_Ectothiorhodospira, g_Halothiobacillus, etc.*), and photosynthetic bacteria (*g_Rhodobacter, g_Rhodococcus, g_Rhodospirillum, etc.*). This indicated that some autotrophic and nitrogen-fixing microorganisms are not involved only in the carbon and nitrogen cycle, but also may participate in the biogeochemical cycles of other elements, thus playing a role in material cycling and energy flow in the micro-ecological environments in saline soils. Microbial communities with different functionalities

jointly regulate and drive the various processes in the element cycling, and play an irreplaceable role in responding to global climate change and maintaining the function and stability of the ecosystems (Bardgett, Freeman & Ostle, 2008; Zhou et al. 2012; Madigan, Bender, Buckley, Sattley & Stahl, 2019).

5. Conclusions

In this study, the modification effect of *in situ* Jerusalem artichoke cultivation on the micro-ecological rhizosphere environment in the saline-alkali soils along the southeast coast of China was elucidated from a microbial perspective. The root system of Jerusalem artichoke was distributed mainly in the soil layer 75-175 mm, avoiding salt damage (high salinity in the top and the deeper layers). The root channels of Jerusalem artichoke improved not only the physical structure of saline soil, but also provided basic conditions for optimizing the soil micro-ecological environment. Rhizosphere exudates (such as carbohydrates, hydrocarbons, acids, etc.), produced by Jerusalem artichoke and soil microbial community, could improve the habitat of saline soil. The community diversity and richness of the autotrophic bacteria and nitrogen-fixing bacteria were greater in the rhizosphere than bulk soils. Many of identified microorganisms participate not only in the carbon and nitrogen cycles, but also in the biogeochemical cycles of other elements, promoting material cycling and energy flow in the micro-ecological environments in saline soils. These findings provided a scientific basis for understanding the biotransformation of carbon and nitrogen in saline soil and the positive effects of Jerusalem artichoke on the micro-ecological rhizosphere environment in saline soil.

Declaration of competing interest

No conflict of interest exists.

Authors' contributions

S.T.Y., L.X.H. and L.M.Q. conceived the ideas and designed methodology; S.T.Y., L.X.H. and G.X.M. collected the data; S.T.Y. analysed the data; S.T.Y. and Z.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figures and tables

Figure 1 An analysis of the variation in root channel area with soil depth in different types of soil.

Note: H- high salinity; M- moderate salinity; L- low salinity; UP- soil under the plants (a circular area with a radius of 13 cm centered on the plant stem); IR- inter-row soil. The data are means (n=5). (A) The variation trend of channel area in different soils with increasing soil depth; (B) Different lower case letters denote significant differences among different soil sample types at a given soil depth (p [?]0.05). The ratios of the root channel area in the 0-200 mm soil layer and the 200-400 mm soil layer for seven different types of soil were indicated above the lower case letters.

Figure 2 Rhizosphere secretions in different soil samples.

Note: H- high salinity; M- moderate salinity; L- low salinity; R- rhizosphere soil; NR- bulk soil; CK- highly saline unplanted control soil. The data are means (n=5). (A) Stacked histograms of the relative proportions of various compounds in different soil samples. The percentages greater than 1% are shown only. (B), (C), (D) Histograms of relative proportions and significant differences in specific rhizosphere secretions in different soil samples. Different lower case letters denote significant differences among different soil sample types for a given secretion (p [?]0.05).

Figure 3 Diversity of soil autotrophic bacteria based on*cbbL* and *cbbM* sequencing.

Note: H- high salinity; M- moderate salinity; L- low salinity; R- rhizosphere soil; NR- bulk soil; CK- highly saline unplanted control soil. The data are means (n=5). (A) and (C) Alpha diversity indices of autotrophic bacteria containing *cbbL* (A) and *cbbM* (C). (B) and (D) Doughnuts of the abundance of genera of autotrophic bacteria containing *cbbL* (B) and *cbbM* (D). (E) and (F) Stacked histograms of the relative proportions of different genera of autotrophic bacteria containing *cbbL* (E) and *cbbM* (F). (G) and (H) LDA Effect Size (LEfSe) of autotrophic bacteria containing*cbbL* (G) and *cbbM* (H).

Figure 4 Diversity of soil nitrogen-fixing bacteria.

Note: H- high salinity; M- moderate salinity; L- low salinity; R- rhizosphere soil; NR- bulk soil; CK- highly saline unplanted control soil. The data are means (n=5). (A) Alpha diversity index of*nifH* -containing nitrogen-fixing bacteria; (B) Hierarchical cluster analysis among samples; (C) Stacked histograms of the percentage of different genera of *nifH* -containing nitrogen-fixing bacteria in different soil samples; (D) LDA Effect Size (LEfSe) of *nifH* .

Figure 5 Correlations among soil physical and chemical properties, rhizosphere secretions and bacterial abundance.

table 1 Abundance and characteristics of important microorganisms

Types of microbes	In CK and NR (relative abundance: NR > R)	In R (relative abundance: R > NR)	General characteristics
Autotrophic bacteria containing *cbbL*	*Gammaproteobacteria* was the main class. The correlation between relative abundance and soil salinity was positive and significant.	*Gammaproteobacteria* was the main class. In moderate and low salinity soils, *Betaproteobacteria* and *Alphaproteobacteria* also had large relative abundance.	Community diversity and richness: NR > R. Relationship between relative abundance and pH: negative correlation (r<-0.6). Soil environments with sufficient oxygen and low CO_2 concentration were conducive to survival.
Autotrophic bacteria containing *cbbM*	*Gammaproteobacteria* and *Alphaproteobacteria* were the main classes. Relationship between relative abundance of *Betaproteobacteria* and salinity: significant negative correlation.	*Betaproteobacteria* and *Alphaproteobacteria* were the main classes. Relationship between relative abundance of *Gammaproteobacteria* and salinity: significant negative correlation.	Community diversity and richness: R > NR. Relationship between relative abundance and pH: negative correlation (r<-0.5). Soil environments with low oxygen and high CO_2 concentration were conducive to survival.
Nitrogen-fixing bacteria containing *nifH*	*Gammaproteobacteria* and *Deltaproteobacteria* were the main classes. Relationship between relative abundance and salinity: significant positive correlation.	*Betaproteobacteria* and *Alphaproteobacteria* were the main classes. Relationship between relative abundance and salinity: significant negative correlation.	Community diversity and richness: R > NR. Relationship between relative abundance and pH: negative correlation (r<-0.5). Soil environments with low oxygen were conducive to survival.

Note: R- rhizosphere soil; NR- bulk soil; CK- highly saline unplanted control soil.