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Improvement of Saline Soil Properties and *Brassica rapa* L. Growth Using Biofertilizers

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Abstract: The decline in agricultural productivity because of soil salinization has become a global problem in recent years. Biofertilizers show great potential for soil improvement as a sustainable strategy; however, their effectiveness in improving saline soils and enhancing plant growth under saline stress is poorly understood. We assessed the effectiveness of biofertilizers in improving saline soils and enhancing crop growth under saline stress and investigated the related potential mechanisms. Changes in soil physicochemical properties, plant physiological parameters, and soil microbial communities were analyzed using pot experiments. The results showed that biofertilizer application reduced total soluble salts in the soil by 30.8% and increased *Brassica rapa* L. biomass by 8.4 times. Biofertilizer application increased soil organic matter, total nitrogen, and available phosphorus by 56.1%, 57.0%, and 290%, respectively. Simultaneously, superoxide dismutase, catalase, chlorophyll a, chlorophyll b, total soluble sugar, and proline levels also increased by 89.5%, 140%, 110%, 190%, and 130%, respectively. Biofertilizers increased the abundance of *Bacillus* and *Planococcus* and decreased the abundance of *Mortierella* and *Aspergillus*, which could potentially be the underlying reason for the promotion of plant growth. Overall, the results of this study demonstrate the efficacy of biofertilizers in improving saline soils and that the application of biofertilizer could greatly promote agricultural production.

Keywords: saline soil; biofertilizer; soil microbial community; *Bacillus licheniformis*; *Halobacillus profundi*; *Brassica rapa* L.

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1. Introduction

Soil quality is a key determinant of land productivity, and the global demand for food is increasing as the world's population grows [1]. Saline soils contain excessive saline and alkaline components, which is a major obstacle to food security and agricultural development [2]. Globally, the area of saline soils was 935 million hectares in 2020 [3], and it has been expanding at a rate of three hectares per minute because of unfavorable conditions, especially insufficient irrigation and longstanding aridity [4]. Soil salinization causes an annual economic loss of $27.3 billion owing to land degradation in irrigated regions [5]. Therefore, it is of urgent necessity to amend saline soils in order to restore and enhance land productivity, ensure food security, and cut potential losses.

The application of organic amendments is a common practice used to improve saline soils [6]. Compost application is effective in improving soil quality [7]. Organic fertilizers can provide a rich source of carbon, energy, and nutrients for soil microorganisms [8]. In addition, organic fertilizers can improve the soil environment and structure, increase

the water-holding capacity of the soil, and promote desalination, as well as reduce soil conductivity and increase its buffering capacity [9]. However, a single organic amendment usually cannot achieve the long-term improvement of saline soils, and has a limited improvement effect on highly saline soils [10].

Biofertilizer is a type of fertilizer that combines both organic fertilizer and functional microorganisms [11]. Through the activities of these microorganisms, biofertilizers can increase the availability and accessibility of nutrients for plant growth and improve crop yield and quality [12]. Previous studies have concluded that biofertilizers can effectively improve saline soils [13,14]. High levels of organic matter can optimize soil structure, increase the activity of soil enzymes, and promote plant growth [15]. In addition, biofertilizers can improve soil quality by accelerating soil microbial community succession [13]. The application of biofertilizers made from various biomasses and beneficial microorganisms could be a valuable method of regulating saline soils [16].

Bacillus licheniformis is a bacterium of high biotechnological value and is widely used [17]. Previous studies have shown that *Bacillus licheniformis* can increase plant biomass under salt stress by modulating plant physiological responses [18–20]. No reports exist on the use of *B. licheniformis* in the preparation of biofertilizers for the improvement of saline soils. *Halobacterium* is a genus that is highly active in saline environments and may have the potential to regulate soil carbon and nitrogen cycling [21]. There are currently no reports indicating that *Halobacterium* has the ability to amend saline soils. In this study, we hypothesized that *Bacillus licheniformis* 4-2 and *Halobacterium profundi* GT42 biofertilizers could effectively improve saline soils. Thus, a pot experiment was carried out in this study with the aim of (1) evaluating the improvement effect of biofertilizers on saline–alkali soil by measuring soil properties and plant biomass and (2) studying the mechanism of biofertilizer improving saline–alkali soil through the interaction of biotic and abiotic factors.

2. Materials and Methods

2.1. Experimental Design

Soil samples were collected from Shihezi, Xinjiang, China (44.32° N, 85.88° E). The soil samples were sieved using a 2 mm mesh for the experiment. The organic fertilizer used in this study was prepared by composting livestock and poultry manure, approximately 300 tons of raw materials, comprising 70% chicken manure, 12% corn straw, 12% bran, and 6% mushroom residue, and was mechanically mixed until the initial water content stabilized around 60%, with a 24-day composting [22,23]. The soils used in this experiment were saline–sodic according to USDA classification [24]. Further information regarding the experimental soils and organic fertilizers is provided in Table S1. *Bacillus licheniformis* 4-2 (NCBI accession number: ON926979) and *Halobacterium profundi* GT42 (NCBI accession number: ON926973) strains were inoculated into organic fertilizer to produce a biofertilizer. The viable counts of *B. licheniformis* and *H. profundi* in the biofertilizers exceeded 2.0×10^8 CFU·g^{-1}.

Pot trials were conducted in a greenhouse located in Langfang City, Hebei Province China, comprising five treatments, each replicated thrice. The sieved saline soil was randomly allocated and uniformly filled into 15 flowerpots (50 × 40 × 30 cm), with each pot containing 21 kg of soil. The five treatments included CK (no fertilizer), OF (100% organic fertilizer, 300 g), BF (*B. licheniformis* biofertilizer, 300 g), HF (*H. profundi* biofertilizer, 300 g), and OM (*B. licheniformis* biofertilizer, 150 g with *H. profundi* biofertilizer, 150 g). All fertilizers were applied as base fertilizers without any additional topdressing. The crop used, *Brassica rapa* L., was initially grown as seedlings at a separate location before being transplanted into the experimental pots. Each pot was planted with 12 seedlings under identical growth conditions (four leaves with a root length of 6 cm). The time period for cultivating seedlings was from 15 March to 31 March 2021. The average temperature in the greenhouse was maintained at 25 °C during the experiment. Except for the fertilization, the other conditions remained the same. The pots were irrigated with 375 mL per day while applying measures to control pests and weeds.

2.2. Soil Sampling and Physicochemical Properties Analysis

Brassica rapa L. was grown for a period of 30 days (from 1 April to 1 May 2021) after transplanting the seedlings. Following harvest, soil samples were collected from each pot and fully mixed after removing vegetation and debris. The soil from each pot was divided into two sub-samples after sieving it through a 2 mm sieve: one was cryopreserved for microbial DNA extraction, while the other was stored in a shaded place for physical and chemical soil analyses. An elemental analyzer (Vario MAX cube) was used to determine the total carbon (TC), total nitrogen (TN), and soil carbon/nitrogen ratio (C/N ratio) of the soil samples [25]. The soil pH was determined in 1:2.5 (w/v) soil water leachate using a pH meter (INESA, Shanghai, China). The active phosphorus (AP) in the soil samples was determined by sodium bicarbonate leach-molybdenum-antimony spectrophotometry according to Chinese standard HJ 704-2014 [26]. The soil organic matter (SOM) in the soil samples was determined by the scorch reduction method according to Chinese standard HJ 761-2015 [27], which was obtained by weighing the weight loss values of air-dried and sieved soils after scorching them in a muffle furnace at 600 °C for 3 h to a constant weight. The total soluble salt (TSS) content in the soil samples was determined according to the Chinese standard NY 1121.16-2006 [28], and the residual values were obtained by weighing the aqueous soil leachate after drying 1:5 (w/v) [11].

2.3. Soil DNA Extraction and Amplicon Sequencing

Primer pairs 338F (ACTCCTACGGGAGGCAGCAG)/806R (GGACTACHVGGGTWTCTAAT) and ITS1 (CTTGGTCATTTAGAGGAAGTAA/ITS2 (GCTGCGTTCTTCATCGATGC) were used to amplify the 16S rRNA gene for bacteria and the ITS gene for fungi, respectively [25]. Following high-throughput sequencing on the Illumina MiSeq PE300 platform, paired-end reads were generated. These reads underwent sequence quality control and pre-processing using USEARCH 11 and VSEARCH 2.22.1 [29,30]. The pre-processed reads were denoised via the unosie3 function to generate the amplicon sequence variants (ASVs). Representative sequences were classified by feature classifiers using the SILVA reference database (version 138.1) and UNITE (version 29.11.2022) in qiime2 (v.2022.8) [31]. Sequences corresponding to chimeras, chloroplasts, mitochondria, and Archaea were excluded. Raw sequencing data with accession numbers SRP371928 and SRP371945 are available from the NCBI database.

2.4. Plant Sampling and Assaying

Upon harvest, the *Brassica rapa* L. yield was evaluated, and plant samples were collected. These samples were divided in half: one portion was dried at 72 °C for 24 h to determine the dry matter content, while the other was used to measure the levels of photosynthetic pigments, antioxidants, and stress resistance substances. Immediately after harvest, the plant chlorophyll (Chl) content was quantified using landscape photometry [32]. The proline content was determined using the ninhydrin method [33]. Following the pretreatment of fresh plants, the soluble sugar content and enzyme activity were measured [34]. The extracts were assessed at an absorbance of 485 nm for total soluble sugars [35]. The efficacy of superoxide dismutase (SOD) was evaluated using the nitro blue tetrazolium chloride method [36]. Catalase (CAT) activity was measured using the enhanced Beers and Sizer technique [37]. Malondialdehyde (MDA) levels were determined using a thiobarbituric acid reaction [34]. Superoxide anion (O2-) activity in the plants were quantitatively determined using a superoxide anion activity assay kit (BC1290, Solarbio Life Science, Beijing, China).

2.5. Statistical Analysis

A total of 15 samples, 5 treatments, and 3 replicates per treatment were used in the experiment. The means and standard deviations were analyzed and plotted using Origin 2021b software (Origin Lab, Northampton, MA, USA). Alterations in the soil physicochemical characteristics and biomass were examined using analysis of variance (one-way

ANOVA), followed by Tukey's test. The microbial alpha diversity was calculated using the R package "vegan" to obtain the Shannon index, Shannoneven index, and Chao index [38]. The differences in alpha diversity between fertilization treatments were calculated using the Wilcoxon rank-sum test, with a statistical significance threshold of 0.05, using SPSS version 26.0 (IBM Corp, Armonk, NY, USA). The degree of similarity in the microbial community was assessed using R software (version 4.1.0, R Foundation for Statistical Computing, Vienna, Austria) based on the nonmetric multidimensional scaling (NMDS) of Bray–Curtis distance matrices. Redundancy analysis (RDA) was used to investigate the effect of soil physicochemistry on the microbial community structure, and the precise localization of the microbiota was determined based on linear discriminant (LEfSe) analysis [25]. The relative contributions of different fertilization scenarios were assessed using a Partial Least Squares Path Model (PLS-PM) [39]. The impact of soil characteristics (pH, TC, TN, AP, and C/N ratio), soil organic matter, soil total soluble salt content, soil microorganisms (the Shannon index, Chao index, and NMDS1 of bacteria and fungi), and plant physiology parameters (SOD, CAT, MDA, O_2^-, Chl. a, Chl. b, total soluble sugar, and proline) on phytomass was evaluated using the "plspm" package (version 0.4.7) in R [40]. The model's goodness-of-fit (GOF) value is 0.87.

3. Results and Discussion

3.1. Amendments of Saline Soil by Biofertilizer

Salinity and plant biomass in saline soil are important indicators that reflect the degree of salinity and the resistance of plants to saline stress. Fertilization reduced the TSS content of each treatment group by 24.2–30.8% ($p < 0.05$) (Figure 1a) as compared with the CK group, with no significant difference between the groups. Organic fertilizers can effectively reduce TSS content, whereas adding PGPR (plant growth-promoting rhizobacteria) to saline soil has a relatively weak effect. Therefore, its organic components may be primarily responsible for the beneficial effects of biofertilizers in saline soils. The application of organic matter improves the soil structure, increases soil bulk density and porosity, and thus promotes the leaching of soil soluble cations [41]. In addition, the organic matter of the organic fertilizers used in this experiment reached 400 g/kg (Table S1).Organic fertilizers introduce large amounts of humus to saline soils, which can adsorb Na^+ into the soil and chelate Ca^{2+} and Mg^{2+} in high-pH environments [15]. Therefore, the application of organic fertilizer has a stabilizing effect, contributing to a decrease in the TSS content.

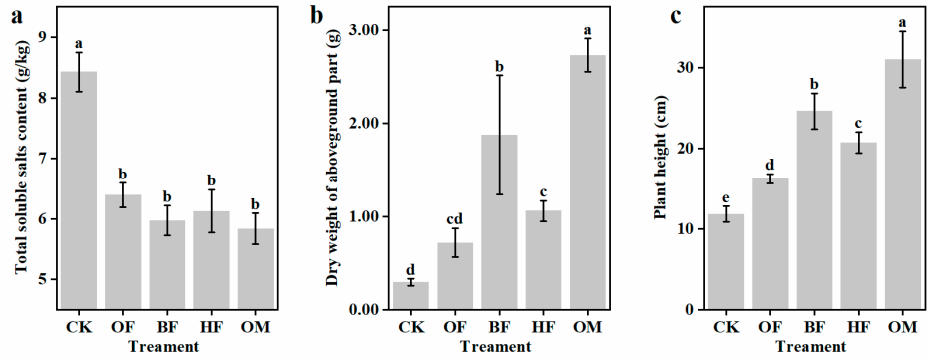

Figure 1. The TSS content in the saline soil (**a**), dry weight of the aboveground part (**b**), and total height (**c**) of the plant. CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*. Different letters represent significant differences according to one-way ANOVA and Student's *t*-test ($p < 0.05$).

Compared to CK, OF, BF, HF, and OM all significantly increased plant biomass ($p < 0.05$), among which OM exhibited the best growth promotion effect. Compared to the CK group, the plant height and dry weight in the OM group rose by 1.6 and 8.4 times, respectively, and 0.5 times and 0.7 times relative to the OF group (Figure 1b,c). Fertilization also significantly increased plant root length and underground biomass ($p < 0.05$) (Figure S1). Based on plant biomass and height, it was concluded that the application of *B. licheniformis* and *H. profundi* yielded better than organic fertilizer. Notably, mixed plant growth-promoting bacteria produced complementary microbial effects [42], which could explain the outstanding performance of OM. Several factors may be responsible for the ability of biofertilizers to stimulate plant growth in saline soils. SOM reduces TSS content, controls the water potential of plant roots, and relieves ion stress in plants [9]. Organic fertilizer boosts plant nutrition by promoting the production of soil aggregates and soil porosity. In addition, *Bacillus* and *Halobacillus* in biofertilizers under salt stress exhibit protease, amylase, nitrogen fixation, and phosphorylation functions and may release indole-3-acetic acid (IAA) to promote photosynthesis and root development [43,44].

3.2. Response of Plant Physiological Characteristics to Fertilization under Salt Stress

To identify the correlation between biofertilizer application and plant growth in saline soils, the physiological properties of the plants, such as antioxidant activity, oxidant accumulation, photosynthetic pigment content, and osmotic regulators, were examined. The results showed that biofertilizers improved overall plant physiology parameters. For example, biofertilizer usage activates the enzymatic activity of plant antioxidants and reduces oxide levels. Compared to that of the CK group, the SOD and CAT of the OM group increased by 60.2% and 89.4%, respectively, while the MDA and O_2^- decreased by 30.1% and 66.6%, respectively (Figure 2a–d). The SOD and CAT effectively removed O_2^- and H_2O_2, respectively, and mitigated plant damage caused by the accumulation of reactive oxygen species (ROS). PGPR, including *B. amyloliquefaciens* and *B. thuringiensis*, induced SOD and CAT production in plants by producing signaling molecules that significantly reduced the accumulation of the oxidative radicals O_2^- and MDA in plant tissues [45]. The levels of antioxidant enzymes in the biofertilizer application group were higher than those in the organic fertilizer alone (Figure 2a,b), suggesting that the added microorganisms might further promote the secretion of plant oxidases. In terms of reducing oxidative toxins, the HF and OM groups exhibited the best performance, which may be related to the addition of *Halobacillus*. Using functional bacteria, particularly *Halobacillus*, biofertilizers are thought to reduce oxidative stress by producing antioxidant enzymes and removing oxidative pollutants.

Fertilization significantly increased the chlorophyll content of the plants ($p < 0.05$) (Figure 2e,f). The single inoculum addition treatment and OF treatment presented minor differences, but the OM treatment group had the highest chlorophyll content ($p < 0.05$). The Chl a and Chl b levels in the OM group were 1.4-fold and 1.1-fold higher, respectively, than those in the control group, indicating that biofertilizers could increase photosynthesis in plants. The photosynthetic rate is susceptible to salt stress, which is closely related to plant development and biomass buildup [46]. Plant chloroplast ion poisoning and decreased chlorophyll content inhibit plant photosynthesis in saline soils [47]. Elevated chlorophyll content in plants can effectively increase photosynthesis, thereby improving stress resistance [48]. Biofertilizers may encourage plants to use water and nutrients efficiently under drought stress and thus restore plant photosynthesis [49,50], which seems to be further enhanced through interactions and cooperation between *B. licheniformis* and *H. profundi* in this present study.

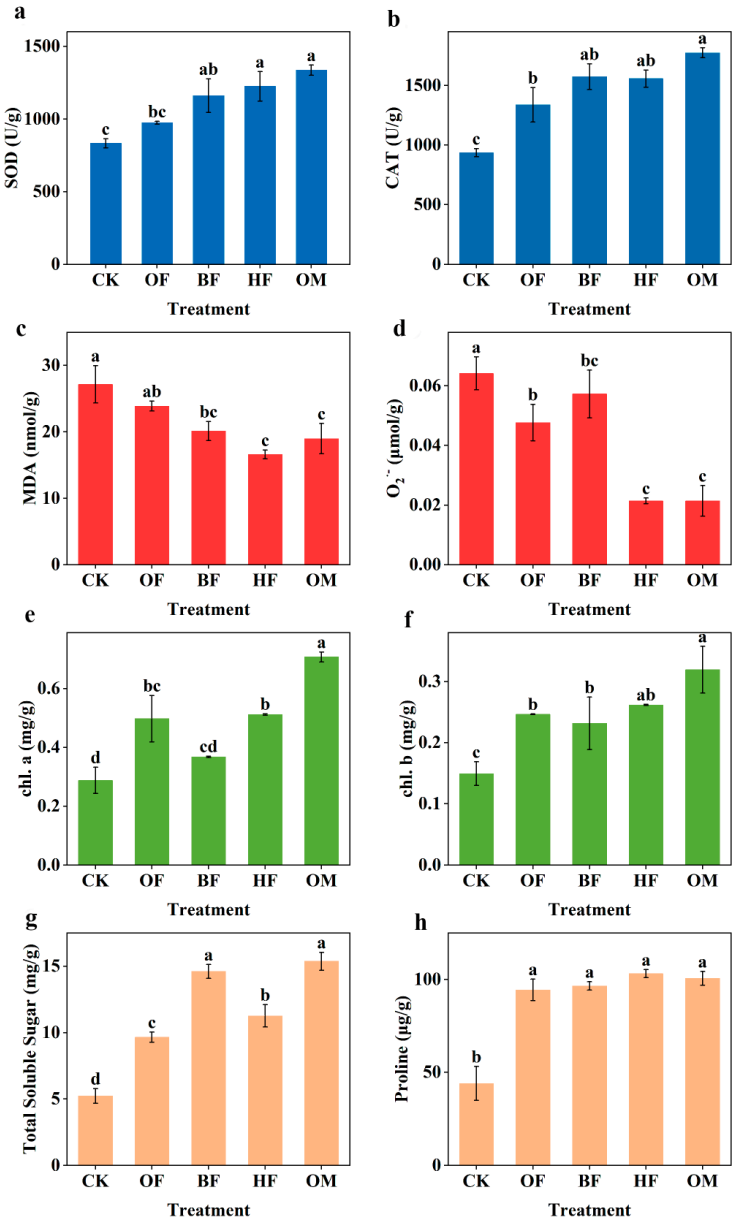

Figure 2. The content of phytohormone SOD (**a**), O_2^- (**b**), MDA (**c**), CAT (**d**), chl. a (**e**), chl. b (**f**), total soluble sugar (**g**), and proline (**h**) inside the plant. CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*. Different letters represent significant differences according to one-way ANOVA and Student's *t*-test ($p < 0.05$).

In addition, fertilization encouraged plants to accumulate total soluble sugars and proline (Figure 2g,h). The proline content was substantially higher in the fertilization treatment groups than in the CK group (p <0.05). Notably, the OM group had a 1.9- and 1.3-times higher plant total soluble sugar and proline content, respectively, than the CK group. Based on these results and previous reports, it was hypothesized that in a low water potential environment, biofertilizers could encourage plants to produce proline and carbohydrates and slow their deterioration, thus causing plants in saline soils to accumulate total soluble sugar and proline [51,52]. Proline and sugars help ease osmotic stress, balance the content of K^+/Na^+ in plants, and preserve plant cell membranes while fostering photosynthesis [53]. Using biofertilizers helps plants accumulate total soluble sugar and proline while decreasing osmotic stress.

3.3. Improvement of Saline Soil Properties by Biofertilizers

Physicochemical indicators were examined to evaluate the effects of biofertilizers on the properties of saline soils. The SOM and TC contents in the soil were dramatically enhanced by fertilization, and the OM group showed the most significant promotion (the SOM and TC contents increased by 56.1% and 28.9%, respectively) ($p < 0.05$) (Figure 3a,b). Biofertilizer application considerably decreased soil pH; however, the biofertilizer treatments did not statistically differ from one another, and the pH of the OM group was much lower than that of the CK and OF groups ($p < 0.05$) (Figure 3b). SOM can also improve aggregate formation and soil structure. The stimulatory effect of biofertilizers and the manipulation of the microbial community can also regulate SOC mineralization [54]. The increase in soil TC may be related to the acidity in saline–alkali soils. An alkaline environment inhibits the conversion of carbonate to carbon dioxide in the soil [55]. This suggests that biofertilizers could improve the carbon sink in saline soil. Biofertilizers slightly reduced the C/N ratio of the saline soil while increasing the TN content ($p < 0.05$) (Figure 3d,e). Compared to the CK group, the TN content in the OM group was elevated by 57.0%. Although the C/N ratio in the fertilization groups was much lower than that in the CK group, no discernible between-group differences were observed. Previous studies have reported that biofertilizers inoculated with *Bacillus* sp. minimize ammonia volatilization (a crucial pathway of nitrogen loss) in alkaline soils [25]. Biofertilizers increased inorganic nitrogen content (NH_4^+-N, NO_3^--N, and NO_2^--N) (Figure S2). The nutritional needs of plants growing in saline soil can be met by addressing the problem of nutrient deprivation in saline soils. Previous studies have shown that soil microorganisms depend on an appropriate C/N ratio [7,56,57]. Microbial community succession in soils may be driven by changes in the C/N ratio during biofertilizer application.

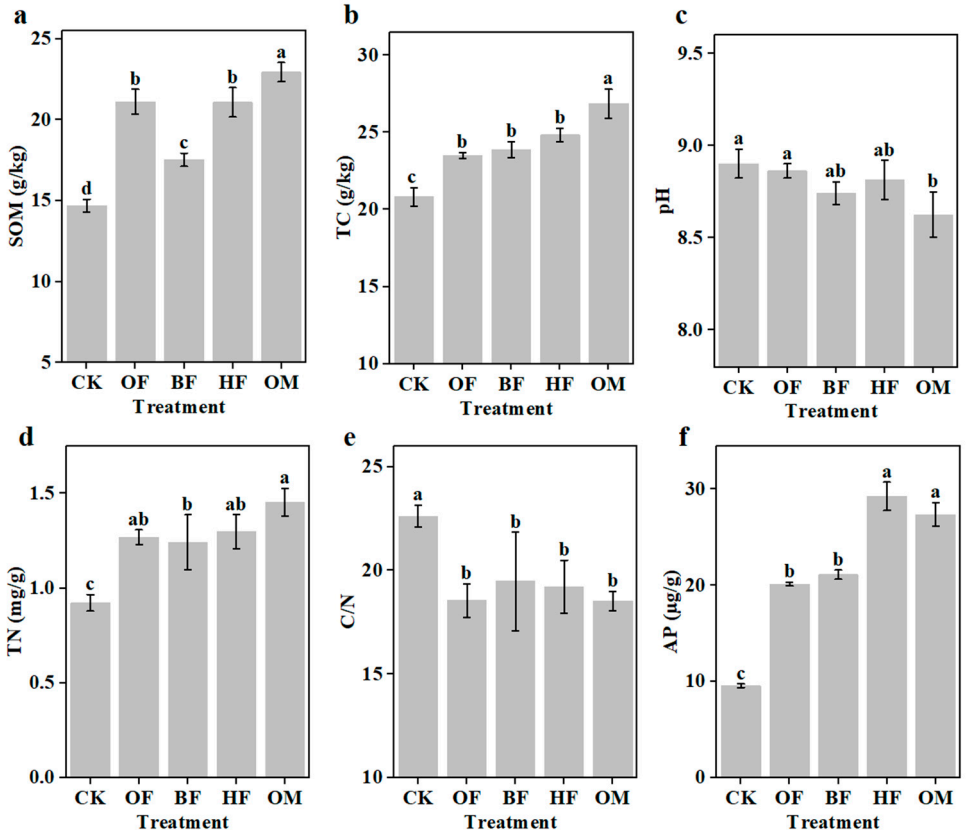

Figure 3. The content of SOM (**a**), TC (**b**), pH (**c**), TN (**d**), C/N (**e**), and AP (**f**) in the saline soil. CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*. Different letters represent significant differences according to one-way ANOVA and Student's *t*-test ($p < 0.05$).

Moreover, fertilizer application significantly affected the soil AP (Figure 3f). Among the fertilizers, HF and OM had the most significant effect on improving the soil AP content compared to that of CK ($p < 0.05$), which increased by 3.1 times and 2.9 times, respectively. Because of the high pH of saline soil, most phosphorus elements exist in the form of ineffective phosphorus, such as $Ca_3(PO_4)_2$, which has low bioavailability and results in the oligotrophy of saline soil [58]. Furthermore, *H. profundi* has the potential to dissolve phosphate and release soluble phosphate ions, and the use of organic fertilizers could significantly raise the AP content of the soil [59–61]. Biofertilizers containing PRPG may effectively improve the nutritional status of saline soils.

3.4. Alteration of Microbial Communities in Saline Soils by Biofertilizers

The correlation between fertilization and the microbial communities in saline soils was examined using amplified sequencing. Fertilization significantly improved the bacterial Chao index ($p < 0.05$) while exerting little influence on the fungal counterpart and hardly affected the Shannon and Shannoneven indexes (Table 1), indicating that fertilization may boost bacterial richness in saline soil. A similar enhancement limited to bacterial richness was observed in the synergistic remediation of saline soil using plants and soil ameliorations [62]. Organic matter input increases microbial diversity in saline soils [63]. The improved soil physicochemical properties described in Section 3.3, especially abundant SOM, available nutrients, and proper pH, could greatly favor bacterial growth.

Table 1. Microbial diversity index table.

Treatment	Chao Index		Shannon Index		Shannoneven Index	
	Bacteria	Fungi	Bacteria	Fungi	Bacteria	Fungi
CK	2378 ± 100 c	415 ± 7 a	6.23 ± 0.04 a	4.09 ± 0.14 a	0.83 ± 0.01 a	0.06 ± 0.01 a
OF	2729 ± 13 a	394 ± 25 a	6.11 ± 0.07 a	3.07 ± 0.48 a	0.76 ± 0.02 a	0.03 ± 0.01 a
BF	2609 ± 131 a	458 ± 24 a	6.13 ± 0.27 a	3.65 ± 0.10 a	0.81 ± 0.03 a	0.04 ± 0.01 a
HF	2563 ± 56 b	410 ± 75 a	5.89 ± 0.62 a	2.90 ± 0.73 a	0.78 ± 0.01 a	0.02 ± 0.01 a
OM	2555 ± 68 b	407 ± 23 a	6.01 ± 0.64 a	3.23 ± 0.13 a	0.79 ± 0.02 a	0.03 ± 0.01 a

Notes: CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*. Different letters represent significant differences according to Wilcoxon rank-sum test ($p < 0.05$).

The results of the NMDS analysis revealed that the microbial community compositions of the fertilization treatment groups differed considerably from those of the CK group (Figure 4). Previous studies have shown that SOM application significantly alters the microbial community structure in saline soils [64]. SOM may have driven the differences in microbial community composition between treatment groups.

There were striking phylum-level differences in community composition under different fertilization regimes. Fertilization promoted the thriving of *Bacteroidota*, *Firmicutes*, *Patescibacteria*, *Myxococcota*, and *Chloroflexi* in the OM group compared with the CK group (68.2%, 246.3%, 27.8%, 188.9%, and 24.4%, respectively). The relative abundance of *Actinobacteriota*, *Gemmatimonadota*, *Acidobacteriota*, *Cyanobacteria*, and *Desulfobacterota* decreased with each fertilization treatment ($p < 0.05$) (Figure 5a). Previous research has shown that *Bacteroidetes* can produce enzymes to break down starch and cellulose [65]; *Chloroflexi* is also an important driver of SOM mineralization [66]. Therefore, soil mineralization may have been aided by using biofertilizers and releasing more inorganic nutrients.

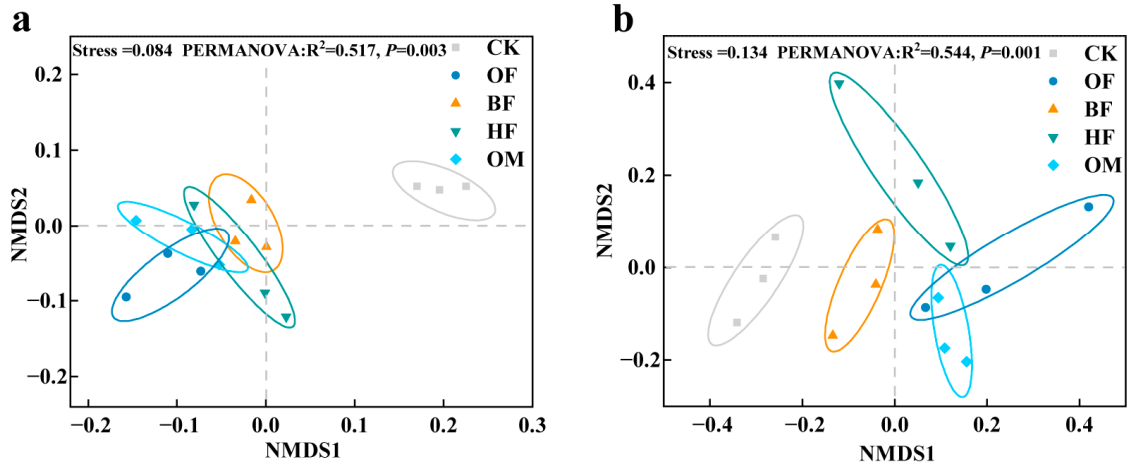

Figure 4. Nonmetric multidimensional scaling (NMDS) ordination plots for bacterial (**a**) and fungal (**b**) community composition at genus level based on the Bray–Curtis distance similarity. CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*.

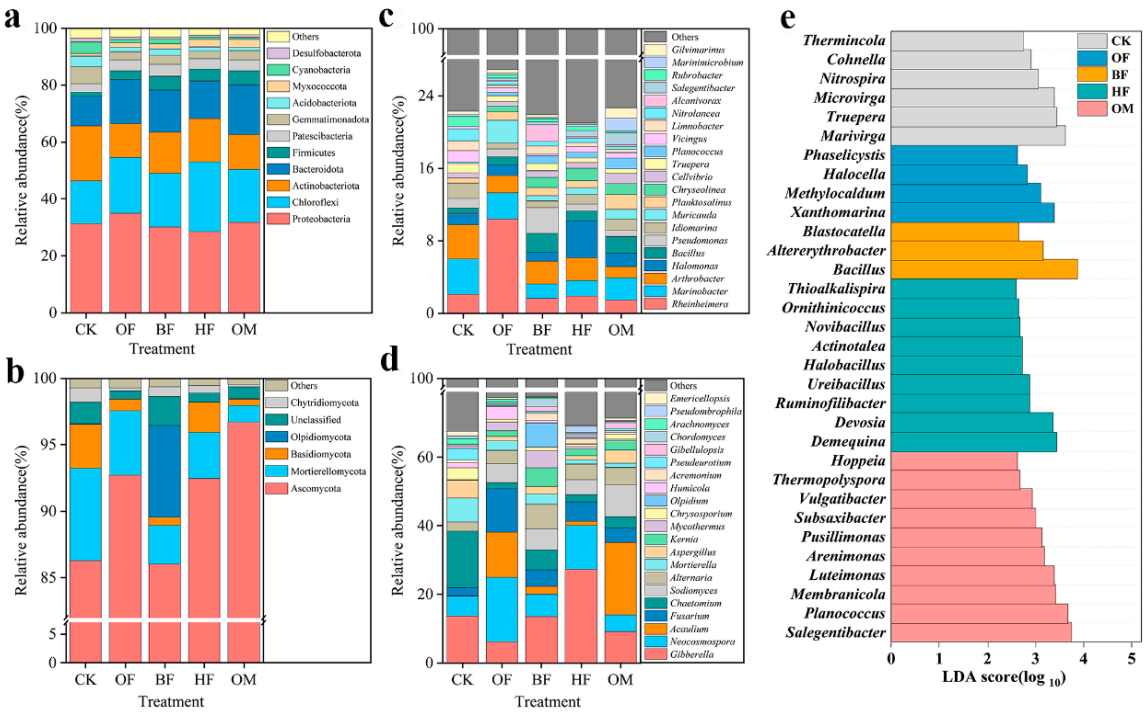

Figure 5. Bacterial community composition at phylum level (>1%) (**a**) and at genus level (>1%) (**c**). Fungal community composition at phylum level (>1%) (**b**) and at genus level (>1%) (**d**). With a threshold value of 2.2, LEfSe determined the degree of divergence between various fertilizer treatments (**e**). CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis and H. profundi*.

Fertilization promoted the thriving of *Bacillus*, *Planococcus*, and *Salegentibacter* compared to the CK group (2.2, 5.1, and 46.6 times, respectively) ($p < 0.05$). Simultaneously, fertilization inhibited the growth of some genera, such as *Marinobacter*, *Arthrobacter*, and *Nitrolancea*, with relative abundances 38.1%, 67.7%, and 74.8% lower than those in the CK group ($p < 0.05$) (Figure 5c). Among these, *Bacillus*, a typical plant growth-promoting bacterium capable of producing signal molecules and secreting auxins [67], can assist in promoting plant development in saline soils. Meanwhile, *Planococcus* could dissolve

phosphorus [68] and thus possibly account for the increased AP content in fertilized soils. Moreover, *Planococcus* may release ACC dehydrogenase, which can encourage microbial colonization and biofilm formation, thereby enhancing the resilience of plants to salt and alkaline stress [69,70].

Regarding fungi, Ascomycota accounted for over 80.0% of the relative abundance in each group, suggesting that fertilization had an insignificant effect on the fungal community at the phylum level. Fertilization resulted in a decline of 81.9%, 84.9%, and 82.6% in the abundance of *Mortierellomycota*, *Basidiomycota*, and *Chytridiomycota*, respectively, in the OM group when compared with the CK group ($p < 0.05$) (Figure 5b). Several plant pathogens originate from *Basidiomycota* [71], which is a possible cause of reduced plant diseases in saline soils.

At the fungal genus level, the OM group had considerably greater relative abundances of *Acaulium*, *Sodiomyces*, and *Kernia* than the CK group (92.7, 256.6, and 9.6 times, respectively), and the *Chaetomium*, *Mortierella*, and *Aspergillus* in the OM group were significantly lower than those in the CK group (4.9, 5.7, and 1.3 times, respectively) ($p < 0.05$) (Figure 5d). Researchers have considered *Mortierella* a potential animal pathogen [72] and *Aspergillus* a typical plant pathogenic bacterium [73]. According to this study, biofertilizers reduce the number of potentially dangerous bacteria, which may also lower the risk of plant diseases.

With an LDA threshold of 2.7, 32 bacterial taxa with statistically significant differences were identified using LEfSe ($p < 0.05$) (Figure 5e). Among them, the OM group contained the most significantly different microorganisms, with a total of ten microorganisms represented by *Salegentibacter*. Only six microbial genera, such as *Marivirga*, showed significant differences in the CK group. Previous studies have found that *Luteimonas* and *Arenimonas* have the potential to promote the aromatization and humification of SOM, which are significantly correlated with the growth of SOM and are potential plant growth-promoting bacteria [74–76]. The application of biofertilizer caused significant differences in the OM treatment group's microorganisms. Therefore, there may have been a deposition effect on SOM humification and an increase in soluble organic matter in the soil.

The pH, TSS content, and C/N ratio negatively affected the microbial community in the biofertilizer treatment groups, whereas SOM, TC, TN, and AP had positive effects (Figure 6). The correlations between the dominant microbial genera and the physicochemical properties of saline soils are illustrated in Figure 7. In the bacterial community, SOM, TC, and TN were linked favorably with *Chryseolinea*, *Cellvibrio*, and *Planococcus*, and were adversely associated with *Nitrolancea*, *Limnobacter*, and *Truepera*. Previous studies suggested that *Chryseolinea* promotes plant growth by regulating nutrient uptake [77], and *Cellvibrio* may facilitate soil humification by producing amylases and cellulases [78].

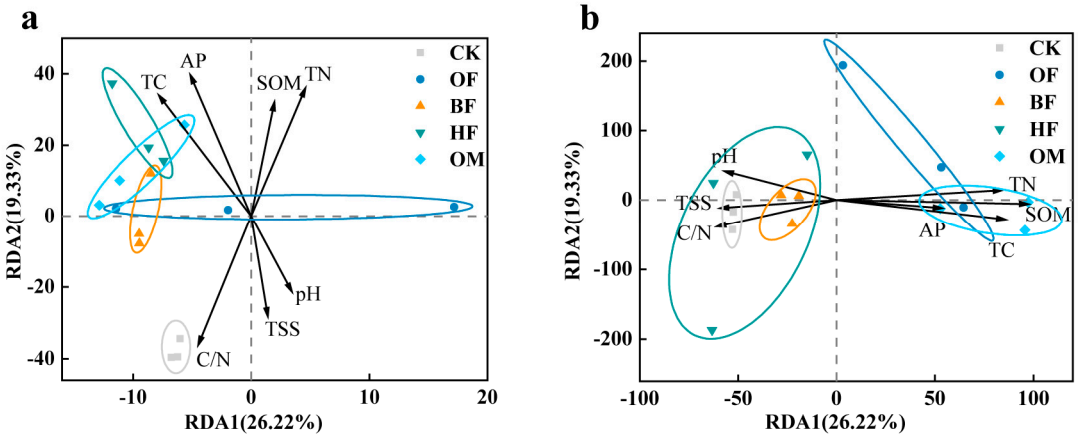

Figure 6. Phylum level redundancy analysis (RDA) of bacterial (**a**) and fungal (**b**) communities with environmental factors. CK, control; OF, organic fertilizer; BF, organic fertilizer with *B. licheniformis*; HF, organic fertilizer with *H. profundi*. OM, organic fertilizer with *B. licheniformis* and *H. profundi*.

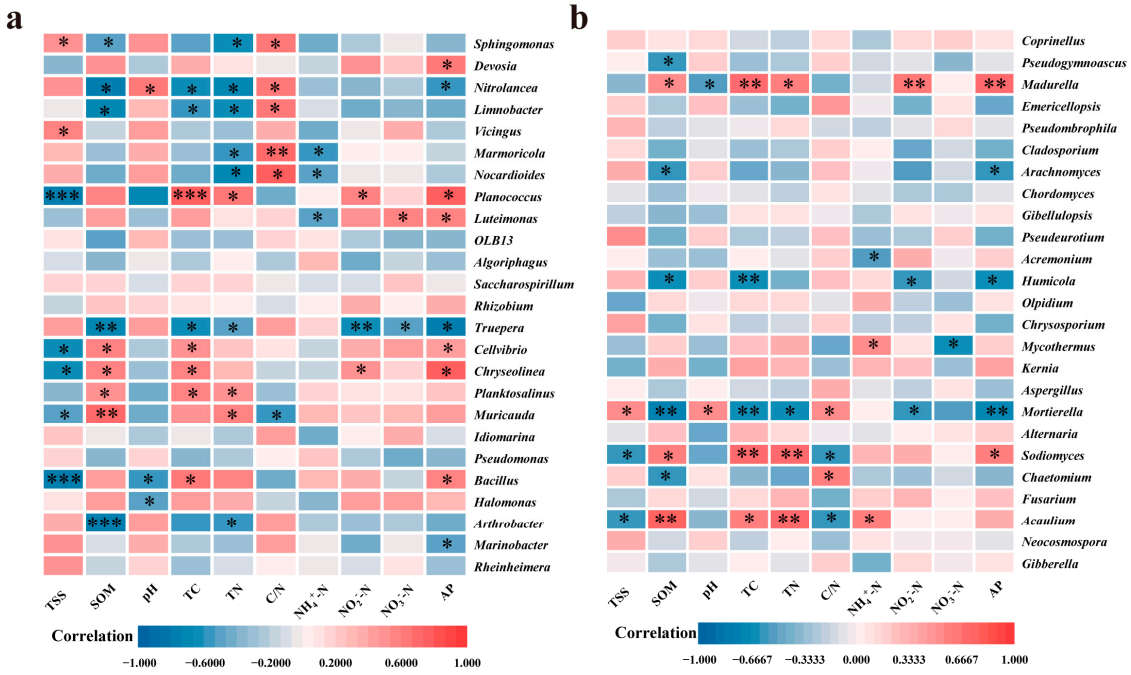

Figure 7. Spearman correlation heatmaps between the top 25 most prevalent genera and the bacterial (**a**) and fungal (**b**) community compositions in the soil at the genus level (* $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, and *** $p \leq 0.001$).

The application of biofertilizer increased soil SOM, TC, and TN, and the relative abundances of *Cellvibrio* and *Chryseolinea* increased the humification of soil cellulose and encouraged the plants to absorb soil nutrients. The TSS content, pH, and C/N ratio were favorably connected with *Sphingomonas* and *Vicingus*, but negatively linked with *Bacillus* and *Planococcus* (Figure 7a). This suggests that biofertilizers improve the aforementioned soil qualities by reducing the stress of soil salinity, which may favor soil bacteria that benefit plant development.

For fungi, SOM, TC, and TN favored the growth of *Madurella*, *Sodiomyces*, and *Acaulium*, while inhibiting the growth of *Mortierella* and *Humicola*. The TSS content, pH, and C/N ratio were favorably associated with *Mortierella*, whereas they exerted a converse effect on *Sodiomyces* and *Acaulium* (Figure 7b). *Sodiomyces* can produce polysaccharides in alkaline environments, which help build extracellular polymers to support plant development [79]. *Mortierella* and *Humicola* are pathogenic fungi that can induce animal and plant disease [80,81]. Biofertilizer application regulates changes in soil microbial diversity and encourages the development of *Sodiomyces* while decreasing the relative abundance of pathogenic bacteria such as *Mortierella* and *Humicola*, both directly and indirectly aiding plant growth, enhancing plant stress resistance, and decreasing the risk of plant diseases.

3.5. Response of Plant Physiological Characteristics to Fertilization under Salt Stress

We investigated the mechanism of biofertilizers for improving saline soil by constructing PLS-PM, linear regression, and random forest models. Combined with the linear regression results (Figure S3), plant physiological conditions were significantly correlated with plant biomass ($p < 0.05$), which suggested that increasing plant biomass in saline soils is one of the keys to regulate biofertilizer application.

Previous studies suggested a link between changes in soil microbial community structure and plant biomass, indicating the changes in soil microbial community structure may be a potential mechanism for increasing plant biomass [82]. This study performed a linear regression analysis to correlate the structure of the soil bacterial community (represented by the NMDS1 axis) with plant biomass and physiological indicators (Figure S4). The results indicated a significant correlation between bacterial community structure and plant

biomass and physiological indicators ($p < 0.05$). Therefore, we believe that the application of biofertilizer can regulate the structure of the soil bacterial community. This change in the structure of the soil microbial community has the potential to regulate the physiological indicators of plants, which in turn improves the plants' resistance to stress in saline soils and leads to an increase in biomass.

The results of the random forest modeling indicated that soil TSS and SOM were the primary abiotic factors influencing bacterial community structure, while fungal diversity was the primary biotic factor influencing bacterial community structure (Figure S5). SOM regulates soil microbial functions by influencing microbial community structure [83]. Fungal diversity influences bacterial community structure through interspecific interactions [84]. Furthermore, the main driver of fungal community structure succession is SOM (Figure 6); therefore, we believe that alterations in SOM may be the key to how biofertilizers drive bacterial community structure in saline–alkali soils. Additionally, the increase in SOM alters fungal biodiversity and drives the succession of bacterial community structure through fungal–bacterial interactions.

This study examined the correlation between SOM and microbial species in saline soils, specifically bacterial genera. A total of 15 bacterial genera were identified as significantly correlated with soil organic matter (Figure S6). *Marivirga* has a strong ability to hydrolyze carbon sources [85]. The relative abundance of soil *Marivirga* was higher in the control treatment group CK, which may have exacerbated the degradation of soil SOM. Several studies have demonstrated a correlation between *Planococcus*, *Membranicola*, and the accumulation of SOM [86]. The high relative abundance of *Planococcus* and *Membranicola* in the OM treatments promoted soil SOM accumulation. Based on the results of LEfSe analyses (Figure 5e), it is suggested that different functional microbial additions drove changes in the abundance of SOM-metabolizing species in the soil, which in turn affected soil SOM accumulation.

The interactions between different factors and biomass during the application of biofertilizers to improve saline soils were studied using a PLS-PM (Figure 8). PLS-PM analysis revealed that physiological factors directly affected plant biomass in the saline soil, followed by soil microorganisms. Fertilizer application significantly increased the SOM content while reducing the TSS content. Changes in the soil environment can effectively drive microbial communities [87]. SOM caused changes in soil physicochemical indicators and microbial diversity, which were significantly correlated with changes in plant physiological parameters. The presence of TSS in saline soils leads to negative physiological responses and stress in plants. Biofertilizer application promoted the succession of soil microbial communities, mainly by increasing the SOM content. Soil microorganisms alter the physiological responses of plants and improve their resistance to saline soil. These pathways promote plant stress tolerance and biomass accumulation in saline soils.

The aim of this study was to assess the effect of biofertilizers on saline soils and predict their pathways in regulating saline soils through pot experiments. It is important to consider the following limitations in this study. Previous studies have shown that fertilizer application can regulate soil sulfur, but pot and field trials differed in effectiveness [88]. The results in this study are based on an analysis of the pot experiment and may not fully represent the actual situation. To verify these results, it is crucial to conduct systematic experiments in a real environment in the future. Additionally, field experiments will be conducted to further evaluate the effects of biofertilizers.

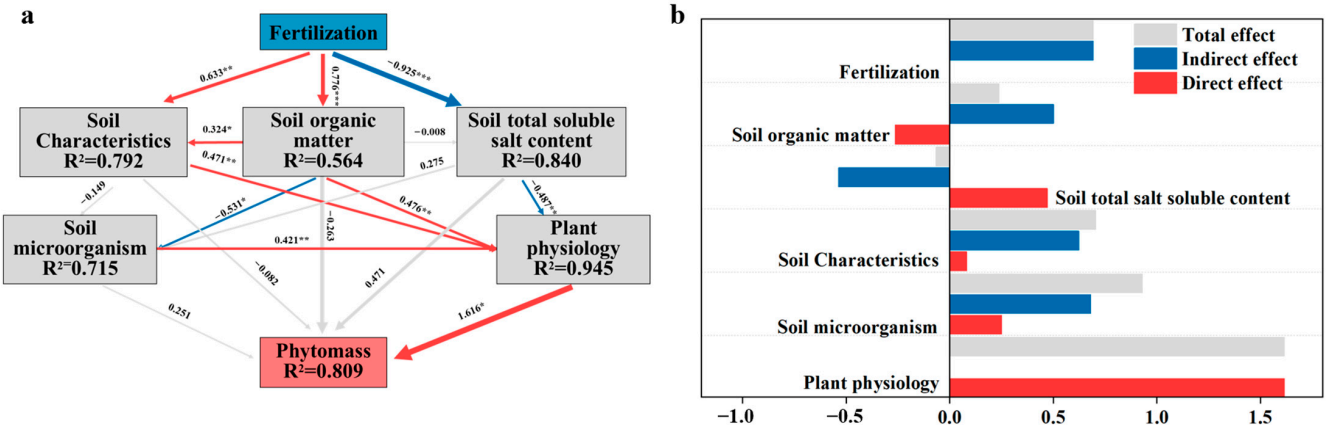

Figure 8. The Partial Least Squares Path Model (PLS-PM) shows the effects of several key factors (soil organic matter, soil characteristics, soil total soluble salt content, soil microorganism, and plant physiology) on the phytomass in saline soil (**a**). The route coefficients are shown by the numbers next to the arrows, and the blue and red arrows indicate adverse and favorable effects, respectively. The size of the route coefficient is also shown by the thickness of the arrows. The path coefficients and determination coefficients (R^2) were generated after 999 bootstrap repeats were computed. Significance levels are denoted by * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$), respectively. The consequences, both direct and indirect, are standardized and obtained from the PLS-PM (**b**).

4. Conclusions

This study demonstrates the efficacy of biofertilizers in ameliorating saline soil, as evidenced by an 8.4-fold increase in plant biomass and a 0.3-fold decrease in TSS. Significant increases in SOM, TC, TN, and AP were also observed in the saline soil, indicating significant improvements in the soil structure and nutrient status. In terms of physiological traits, biofertilizer application increased the levels of SOD, CAT, Chl a, Chl b, total soluble sugars, and proline and reduced MDA and O_2^- levels. These changes in physiological traits may have resulted in improving salt stress tolerance and in higher plant biomass. Moreover, the application of biofertilizers alters the soil microbial community composition by increasing the abundance of *Bacillus* and *Planococcus*, which may benefit soil quality and plant growth. Meanwhile, the abundance of phytopathogenic fungi such as *Mortierella* and *Aspergillus* declined. These results indicate that biofertilizers effectively improve saline soils and enhance plant growth under saline stress. Consequently, biofertilizers may be a promising strategy for improving saline soils and enhancing agricultural production.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/su16052196/s1, Table S1: Properties of saline–alkali soil and organic fertilizers; Figure S1: Plant root length (a) and dry weight of underground part (b) of plant; Figure S2: The content of NH_4^+-N, NO_3^--N, and NO_2^--N in the saline–alkali soil. Figure S3. Linear regression relationship between the levels of different plant physiological indexes and the amount of dry weight of plant above-ground parts. Figure S4. Linear regression relationships between bacterial microbial community structure (NMDS1) and different plant indicators. Figure S5. Random forest modeling of the effect of different indicators on bacterial community structure (NMDS1), (a) prediction of model accuracy using linear regression, (b) the impact of unused factors on bacterial community structure can be measured by the incMSE value. Figure S6. Linear regression relationship between SOM and bacterial taxa (genus level).

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