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Porous Minerals Improve Wheat Shoot Growth and Grain Yield through Affecting Soil Properties and Microbial Community in Coastal Saline Land

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Abstract: Soil salinization has become a major environmental factor severely threatening global food security. The application of porous minerals could significantly ameliorate soil fertility and promote plant productivity under salt stress conditions. However, the effects of porous minerals on improving the salt resistance of grain crops in coastal saline soils is not fully studied. In this work, the shoot growth and grain yield of wheat plants grown in coastal saline fields, respectively amended with the four naturally available porous minerals, diatomite, montmorillonite, bentonite and zeolite, were assessed. The application of porous minerals, especially zeolite, significantly improved the biomass and grain yield of wheat plants under saline conditions, as demonstrated by the augmented plant fresh mass (14.8~61.2%) and increased seed size (3.8~58.8%) and number (1.4~57.5%). Soil property analyses exhibited that porous-mineral amendment decreased soil sodium content and sodium absorption ratio, and increased soil nutrients in both the rhizosphere and nonrhizosphere of wheat plants. Further quantitative-PCR and 16S high-throughput sequencing analysis revealed that porous-mineral application also remarkably increased the abundance of bacterial 16S rRNA (0.8~102.4%) and fungal 18S rRNA (89.2~209.6%), and altered the composition of the soil microbial community in the rhizosphere of wheat. Our findings suggest that zeolite could be used as an ideal salt soil amendment, and the changes in soil properties and microorganisms caused by the application of porous minerals like zeolite improved the salt resistance of wheat plants in coastal saline land, leading to increased shoot growth and seed production.

Keywords: mineral material; coastal saline soil; wheat; soil properties; 16S rRNA high-throughput sequencing

1. Introduction

With the rapid growth and development of the world population and economy, the demand for food production is increasing. In addition to other adverse environmental factors, high salt is a major threat to global food security, especially in Asia, Africa and the Middle East [1]. Over the past few decades, from 1980 to 2018, an area of approximately 11.73 million km^2 in nonfrigid zones has been affected by salt, and it was estimated that by 2050, approximately 50% of the world's arable land will be affected by salinization [1]. In China, saline land covers an area of 36 million hectares, representing about 5.0% of the total available land in the country. Therefore, to alleviate the shortage of cultivated land, it is imperative to bring barren salt-affected soils into cultivation, although the reserved resources in terms of arable land are scarce [2].

Soil amendment has been taken as one the most common approaches for centuries to improve the properties of soil and the yield of crops [3]. Both organic and inorganic amendments, such as organic waste, straw, biochar [4–6] and gypsum, have been successfully used to reclaim salt-affected land [7,8]. Among them, the environment-friendly and locally available porous minerals, i.e., montmorillonite, bentonite and zeolite, were found to mainly function through affecting soil physicochemical properties, such as pH values, nutrient availability, soil organic carbon (SOC) retention and stability, microaggregate formation, and soil microbial assemblage structure and activity [9]. They also worked in the improvement of fertilizer utilization efficiency and remediation of soil pollution. Zeolite was reported to be able to improve nitrogen (N) utilization efficiency and increase N uptake via regulating ammonium (NH_4^+-N) retention [10]. Montmorillonite and bentonite were able to remove heavy metals from water [11]. Bentonite also showed remarkable effects on the improvement of saline soil [12]. Recently, it was reported that the application of zeolite together with rock phosphate or silica calcium soil conditioner significantly increased wheat yield and improved soil properties in saline soils [13].

Soil microorganisms play an important role in both soil health and plant growth [14]. To date, many studies focused on the improvement of soil physicochemical properties and plant growing conditions via soil amendments have been carried out [13,15]. And a close relationship among soil physicochemical properties, host plants and soil microorganisms was observed [16]. The rhizosphere, a microenvironment affected by plant–microbe–soil interactions and where nutrients are exchanged and transferred between the roots and external soils of plants, was found to be one of the areas which harbored the most active microorganisms [17]. The physicochemical and biological properties between rhizosphere and nonrhizosphere soils in terms of microbial community were different [18]. Changes in soil properties and the habitats provided for microbes with the addition of porous minerals might enhance microbial abundance and diversity, which ultimately affects the growth of plants. The application of vermicompost, humic acid fertilizer, cotton stubble return and biochar all altered the community of soil microbes and the contents of carbon (C) and N in coastal saline fields [18].

Saline-alkali soil is widely distributed in the Yellow River Delta (YRD), one of the three estuarine deltas and important land resources in China [19]. Due to the high salinity and low organic matter in this fragile ecosystem, coastal saline soils generally exhibit poor structure stability, which is not beneficial for the growth and yield improvement of crop plants [20]. As one of the major staple crops in China, wheat is moderately tolerant to salinity, with a soil salinity threshold of 600 $\mu S\ cm^{-1}$ [21]. Although the effects of mineral amendment strategy on soil property and plant growth have been investigated, the effects of different porous minerals on wheat shoot growth and grain yield, as well as on the properties and microbial community structure in rhizosphere and nonrhizosphere soils in coastal saline area, are not well studied.

2. Materials and Methods

2.1. Experimental Location and Soil Sampling

Field experiments in this study were carried out at the Modern Agriculture Experiment and Demonstration Base of Shandong Academy of Agricultural Sciences located on Yellow River Delta (YRD), Shandong Province, China (37°17′ N, 118°36′ E). This location is situated in a typical region of the YRD, characterized by a warm temperate continental monsoon climate with an annual rainfall of 590.9 mm and pan evaporation over 1500 mm (about 70% of the total annual precipitation falls between June and September). The mean annual temperatures ranged from 11.5 to 12.4 °C, with a minimum and maximum yearly average temperature of 4.1 °C in January and 26.6 °C in July [22]. The dominant soil type is salic fluvisol with a clay loamy texture, and the crop rotation system is dominated with winter wheat and summer maize [23]. Before the sowing of wheat in October 2021, soil samples (0–20 cm in depth) were randomly collected, air-dried and sieved (2 mm mesh) for subsequent physicochemical property analysis.

2.2. Field Experiment Design

To explore the effects of different porous-mineral applications on the growth and grain yield of wheat in the coastal saline area, diatomite, montmorillonite, bentonite and zeolite were chosen in this study. Five treatments, designated as control (CK), diatomite, montmorillonite, bentonite and zeolite, were arranged in a randomized complete block design. All treatments with three repetitions were analyzed in the same way. The chemical properties of the control soil and amendments are shown in Table 1.

Table 1. Physiochemical property analysis.

Amendments [1]	pH	EC (μs cm^{-1})	Total N (mg kg^{-1})	Organic Matter (mg kg^{-1})
Control Soil	8.0	632.0	92.0	12.2
Diatomite	7.4	901.0	1.1	0.3
Montmorillonite	8.3	322.5	38.1	1.9
Bentonite	7.8	358.5	205.0	4.4
Zeolite	7.6	340.5	40.3	0.3

[1] The pH value, electrical conductivity (EC), total nitrogen (N), organic matter of control soil, diatomite, montmorillonite, bentonite and zeolite are examined.

Seeds of an elite wheat cultivar "Jimai 22" were sown on 28 October 2021, with a seeding rate of 600 kg ha^{-1} at a row space of 20 cm. The plot size in each treatment was 7.5 m^2 (3 m × 2.5 m). All amendments were applied at a dosage of 2.67 t ha^{-1}, equivalent to 1% of the soil weight in a depth of 0–20 cm. Diatomite was provided by the Korean Autonomous County Jinyuan Diatomite Products Co., Ltd. (Changbai, Jilin, China), while montmorillonite, bentonite and zeolite were produced by the Fengju mineral products processing plant (Shijiazhuang, Hebei, China). For each plot, both compound fertilizer and phosphate fertilizer (calcium superphosphate) were applied as a basal fertilizer with an amount of 800 kg ha^{-1}. The compound fertilizer was composed of sulfur (S) ≥ 10% and N ≥ 25% (urea N ≥ 11%, NH_4^+-N ≥ 14%) (Tai'an Huijin Fertilizer Co., Ltd., Tai'an, Shandong province, China). Both mineral amendments and fertilizers applied were evenly spread in each plot and mixed into the soil via deep plowing. Field irrigation mainly depended on natural rainfall and was only irrigated on 23 April 2022, at the stem elongation stage during the growing season.

2.3. Sampling and Measurements

For wheat biomass and grain yield analysis, plant samples were, respectively, collected on 21 April 2021, at the stem elongation stage (176 days after sowing), and on 15 June 2021, at the maturity stage (230 days after sowing). At the stem elongation stage, a total number of 10 plants randomly collected in each plot from three repetitions were used to determine plant height and fresh mass. At the maturity stage, a total number of 20 plants randomly harvested in an area of 0.25 m^2 in each plot were used to assess the biomass and grain yield. For 100-grain weight assays, three groups of 50 grains from each plot were used to conduct the measurements.

For soil sample collection at the stem elongation stage, a total number of 20 plants in each plot were randomly uprooted, and rhizosphere and nonrhizosphere soils were separately collected as described previously [24]. Specifically, rhizosphere soil was obtained via vigorously shaking the plants to separate the nonrhizosphere soil that was not tightly adhered to the roots. Soil pH and electrical conductivity (EC) were, respectively, determined at a soil/water ratio of 1:5 using a pH meter (Mettler S210, Columbus, OH, USA) and EC meter (DDS-11A). Soluble monovalent cation (K^+, Na^+), divalent cation (Ca^{2+}, Mg^{2+}) and anion (PO_4^{3-}) in air-dried soil were extracted with distilled water (5:1 water-to-soil ratio) and, respectively, analyzed with a flame photometer (FP640), atomic absorption spectrophotometer (TAS-986) and Smartchem analyzer (Smartchem200, WESTCO, Guidonia, Italy). The K^+/Na^+ ratio and sodium absorption ratio (SAR) were calculated as described previously [25]. Soil inorganic N, including NH_4^+-N, nitrite (NO_2^--N) and nitrate (NO_3^--N), was determined as described by Ma et al. (2015) [26]. Total N was determined with the Kjeldahl method using an automatic Kjeldahl apparatus (KDY-9830) [27]. Soil organic matter was measured according to the $K_2Cr_2O_7$ colorimetric oxidization method [28].

2.4. Soil Microbial Analysis

Total soil DNA was isolated using the FastDNA® SPIN Kit for Soil (MP Biomedicals, Solon, OH, USA) according to the manufacturer's protocol. DNA concentrations were determined with the spectrophotometer Nanodrop 2000c (Thermo-Fisher, Waltham, MA, USA).

The copy numbers of 16S and 18S rRNA genes of bacteria and fungi based on the fluorescence intensity of the SYBR Green I dye were quantified using the BioRAD CFX96 fast real-time PCR system (Applied Biosystems, California, CA, USA) with the primer pairs 341F/517R and NS5/NS6, respectively [29]. For each reaction, a total volume of 20 mL TB Green™ Premix Ex Taq™ II (TaKaRa, Kyoto, Japan) supplemented with 0.8 mL of each primer and 1 mL of a soil DNA template was established. Thermal cycling conditions were as follows: preincubation at 50 °C for 2 min; pre-denaturation at 95 °C for 10 min; then reaction for 40 cycles consisting of denaturation at 95 °C for 30 s, annealing at 57 °C for 40 s and extension at 72 °C for 40 s (for bacteria); annealing at 60 °C for 30 s and extension at 72 °C for 30 s (for fungi); then followed by melting curve analysis at 65–95 °C (0.5 °C per reading). Standard curves for the genes were obtained using serial dilutions of linearized plasmids (pTZ57R/T, Fermentas, Waltham, MA, USA) containing the target gene amplified from environmental clones (R^2 = 0.99 for all standard curves).

For high-throughput sequencing analysis, a fragment spanning the V3 and V4 regions of bacterial 16S rRNA was amplified using the universal primers 341F (5′-CCTAYGGGRBGCASCAG-3′) and 806R (5′-GGACTACNNGGGTATCTAAT-3′), where a barcode is an eight-base sequence unique to each sample. PCR reactions were performed in triplicate in a 20 µL mixture containing 4 µL of 5 × FastPfu Buffer, 2 µL of 2.5 mM dNTPs, 0.8 µL of each primer (5 µM), 0.4 µL of FastPfu Polymerase, and 10 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, USA) according to the manufacturer's instructions. Purified PCR products were quantified with Qubit®3.0 (Life Invitrogen, Carlsbad, CA, USA), and every twenty-four amplicons whose barcodes were different were mixed equally. Pooled DNA product was used to construct an Illumina Pair-End library following Illumina's genomic DNA library preparation procedure. Then, the amplicon library was paired-end sequenced on an Illumina MiSeq platform (Shanghai BIOZERON Co., Ltd., Shanghai, China) according to the standard protocols. The raw reads were deposited into the NCBI Sequence Read Archive (SRA) database.

Raw fastq files were first demultiplexed using in-house perl scripts according to the barcode sequences' information for each sample with the following criteria: (i) the 250 bp reads were truncated at any site receiving an average quality score < 20 over a 10 bp sliding window, discarding the truncated reads shorter than 50 bp; (ii) exact barcode matching, 2 nucleotide mismatch in primer matching and reads containing ambiguous characters were removed; (iii) only sequences with an overlap of longer than 10 bp were assembled according to their overlap sequence. Reads which could not be assembled were discarded. OTUs were clustered with 97% similarity cutoff using UPARSE (version 7.1), and chimeric sequences were identified and removed using UCHIME. A representative sequence for each OTU was picked and classified with the Ribosomal Database Project (RDP) classifier (version 11.5). Graphical representation of the relative abundance of bacterial diversity from phylum to species was visualized using a Krona chart. Hierarchical clustering analysis was performed with ggplot2 based on the Bray–Curtis similarity coefficient. Canonical correspondence analysis (CCA) was employed to explore the relationship between environmental factors and bacterial communities depending on the unimodal response of community data to the environmental variables.

2.5. Statistical Analyses

The differences in means of biomass and yield of wheat and soil properties (pH, EC, soluble ions, K^+/Na^+, SAR, inorganic N, soluble P, 16S and 18S copies) among different treatments were tested using one-way analysis of variance (ANOVA) and least significant difference (LSD) with a significance level of 5%. Statistical analyses were performed using SPSS (version 16.0, USA), while the graphs were created with Origin 9.0. All results were reported as means $\pm$ SD (standard deviation) on a dry soil weight basis.

3. Results

3.1. Porous Minerals Improved Shoot Growth and Grain Yield of Wheat Plants in Coastal Saline Soil

To understand whether the application of porous minerals would affect the growth and seed yield of grain crops in coastal saline land, we examined the biomass production and grain yield of wheat cultivar "Jimai 22" grown in the field trial base located on the YRD. Four porous minerals, diatomite, montmorillonite, bentonite and zeolite, with different chemical properties were chosen as soil amendments (Table 1). The growth phenotypes of wheat plants at both the stem elongation and harvesting stages were examined and compared. We found that at the stem elongation stage, the overall growth of wheat plants in plots treated with different porous minerals was obviously better than that of wheat plants grown in the control (CK) plots without any porous-mineral treatment (Figure 1A). The fresh mass of wheat plants grown in plots amended with diatomite, montmorillonite, bentonite and zeolite was all dramatically higher than that of plants grown in the control plots, although increased plant height was observed only in wheat plants grown in the plots amended with zeolite (Figure 1B–D). Compared to that of wheat plants grown in the control plots, the fresh mass of wheat plants grown in plots amended with diatomite, montmorillonite, bentonite and zeolite increased 18.0%, 20.5%, 26.5% and 59.6%, respectively (Figure 1D). These observations suggest that porous-mineral application promoted the vegetative growth of wheat plants under salt stress conditions.

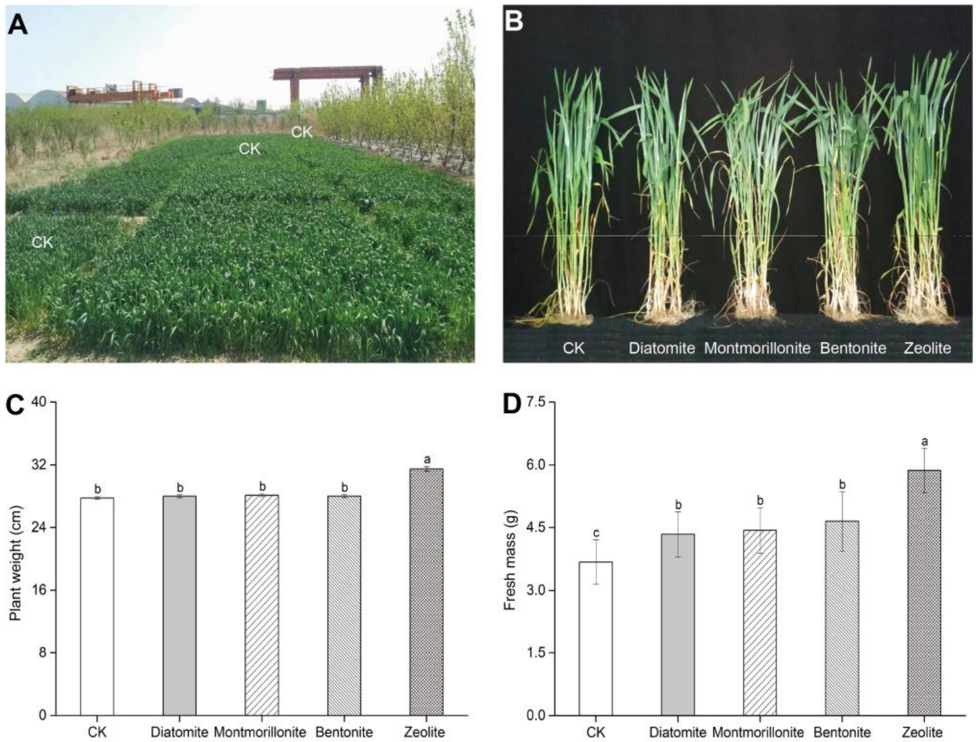

Figure 1. Porous minerals promoted vegetative growth of wheat. Plant height and fresh mass of wheat plants grown in control (CK) and different porous-mineral-treated plots at stem elongation stage were compared. (**A**) An overview photo showing the growth states of wheat plants in the experimental field. (**B**) Phenotypes of representative wheat plants. (**C**) Plant height. (**D**) Plant fresh mass. Values were means and standard deviations of three replicates ($n = 3$). Different lowercase letters denote significant difference among different porous-mineral treatments ($p < 0.05$).

We also compared the biomass and grain yield of wheat plants at the maturity stage. Similarly, porous-mineral treatments significantly improved the shoot growth of wheat plants (Figure 2A–C). Plants grown in plots amended with porous minerals, especially those in the plots amended with bentonite and zeolite, which also exhibited increased plant height, produced greater biomass than those grown in the control plots (Figure 2B,C). In addition, the grain yield of plants grown in plots treated with bentonite and zeolite was remarkably higher than that of plants grown in the CK and diatomite- and montmorillonite-treated plots (Figure 2D–G). Specifically, the ear length, ear weight and ear grain weight, as well as ear grain number and 100-grain weight, of plants grown in plots treated with bentonite and zeolite increased 10.1% and 16.9% (length), 8.2% and 63.9% (weight), 8.2% and 63.9% (grain weight), 13.5% and 57.5% (grain number), and 6.0% and 8.8% (100-grain weight), respectively (Figure 2E–I).

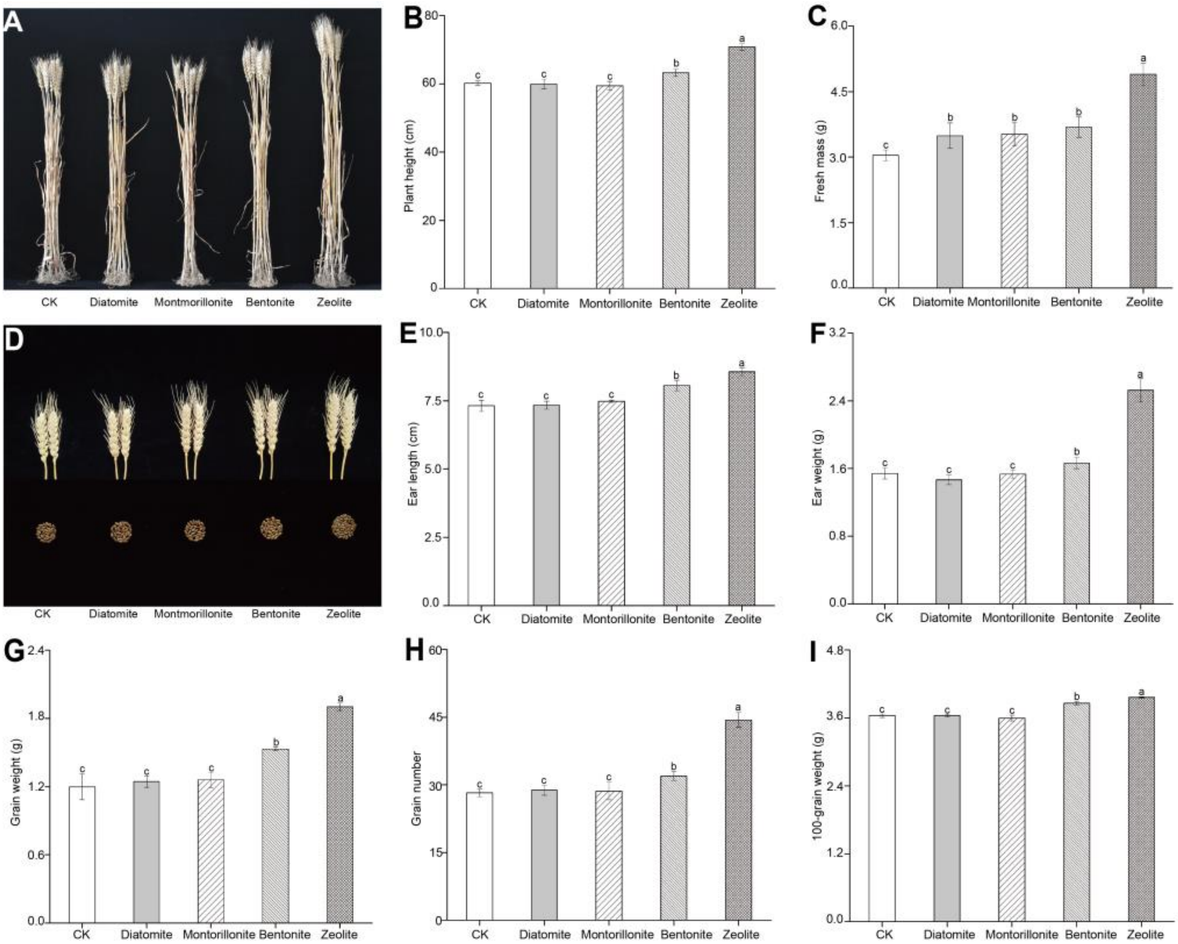

Figure 2. Porous minerals improved wheat biomass and grain yield at the maturity stage. (**A**) Phenotypes of representative wheat plants at maturity grown in control (CK) and different porous-mineral-treated plots. (**B**) Plant height. (**C**) Plant fresh mass. (**D**) Ear and seed sizes. (**E**–**I**) Ear lengths, ear weights, ear grain weights, ear grain numbers and 100-grain weights. Values were means and standard deviations of three replicates (n = 3). Different lowercase letters denote significant difference among different porous-mineral treatments (p < 0.05).

3.2. Porous Minerals Significantly Affected Rhizosphere and Nonrhizosphere Soil Properties

To understand the effects of different porous minerals on soil properties, we collected the rhizosphere and nonrhizosphere soils of wheat plants at the stem elongation stage and examined the soil pH, EC and soluble ion contents. Compared to that in the control samples, soil pH in the rhizosphere of wheat plants grown in plots amended different porous minerals increased 1.4% to 4.3%, but no significant difference was observed in the nonrhizosphere soil, except for a significant reduction in the sample from plots treated with diatomite (Figure 3A). Soil EC in the sample from plots treated with zeolite was significantly lower than that in the control sample, with a decrease of 18.8% in rhizosphere soil and 28.8% in nonrhizosphere soil (Figure 3B). However, soil EC increased 42.5% and 18.2% in the rhizosphere soil amended with diatomite and montmorillonite, and 26.9% in the nonrhizosphere soil amended with diatomite (Figure 3B). The soluble K^+ content increased 21.0% in the rhizosphere soil amended with montmorillonite, and 20.6%, 28.5% and 9.5% in the nonrhizosphere soil amended with diatomite, montmorillonite and bentonite, respectively, but decreased 10.5% in the rhizosphere soil amended with zeolite (Figure 3C). The soluble Na^+ increased 100.7% and 5.8% in the rhizosphere soil from plots amended with diatomite and montmorillonite, respectively, and 49.0% in nonrhizosphere soil from plots amended with diatomite, but decreased 24.5% and 57.1%, and 31.5% and 60.2% in the rhizosphere and nonrhizosphere soil from plots amended with bentonite and zeolite (Figure 3D). Similarly, the soluble Ca^{2+} decreased 17.0% in the rhizosphere soil from plots amended with zeolite and increased 12.7%, 20.7% and 24.0% in the nonrhizosphere soil from plots amended with diatomite, montmorillonite and bentonite, respectively (Figure 3E). In comparison with that in the control samples, soluble Mg^{2+} contents increased 19.9% and 15.4% in the rhizosphere soil from plots amended with diatomite and montmorillonite, respectively, but decreased 36.1% from plots amended with zeolite, and increased 61.0%, 45.7% and 27.4% in the nonrhizosphere soil from plots amended with diatomite, montmorillonite and bentonite (Figure 3F).

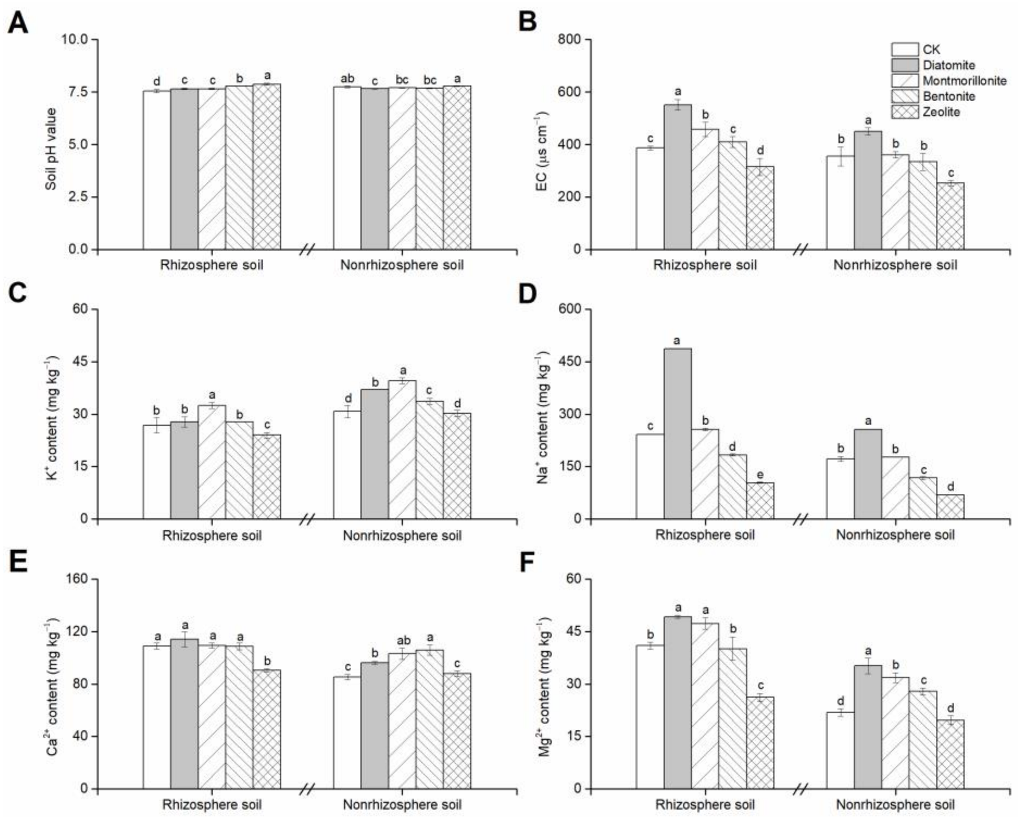

Figure 3. Porous minerals influenced soil properties. (**A**) Soil pH values. (**B**) Electrical conductivity (EC). (**C–F**) K^+, Na^+, Ca^{2+} and Mg^{2+} contents. Values were means and standard deviations of three replicates ($n = 3$). Different lowercase letters denote significant difference among different porous-mineral treatments ($p < 0.05$).

We further analyzed the K^+/Na^+ ratio in the soils collected in the control (CK) and different porous-mineral-treated plots. An increase of 15.9–117.5% in the K^+/Na^+ ratio was observed in all the soil samples from plots amended with different porous minerals, except for the samples from plots amended with diatomite (Figure 4A). Regarding SAR detection, in both rhizosphere and nonrhizosphere soil from plots amended with diatomite, a 92.0% and 32.8% increase was observed, and from plots amended with bentonite and zeolite, and from plots amended with montmorillonite, bentonite and zeolite, a 22.8% and 51.4%, and 7.2%, 38.1% and 59.9% decrease in SAR was detected, respectively (Figure 4B).

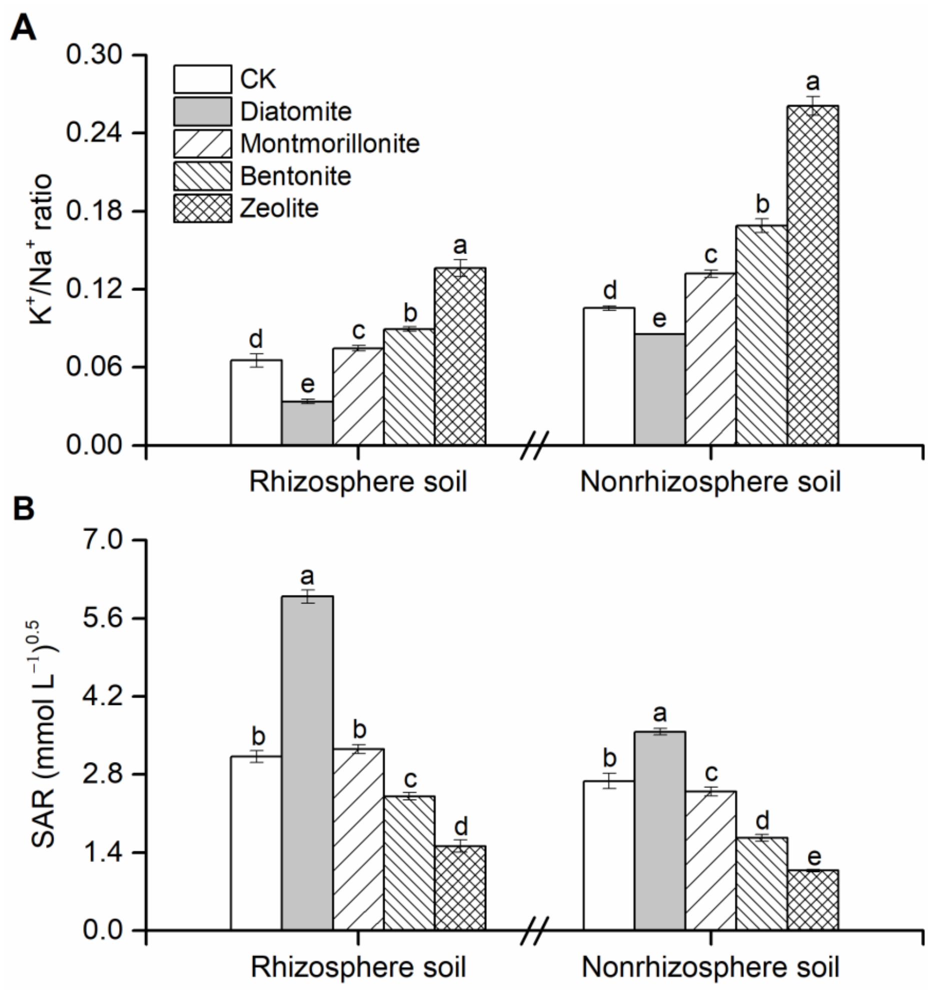

Figure 4. Porous minerals influenced soil property. (**A**) K^+/Na^+ ratio. (**B**) Sodium adsorption ratio (SAR). Values were means and standard deviations of three replicates (n = 3). Different lowercase letters denote significant difference among different porous-mineral treatments ($p < 0.05$).

3.3. Porous Minerals Improved Soil Nutrients in the Coastal Saline Land

To understand whether the application of different porous minerals would also affect the soil nutrients in coastal saline land, we compared the inorganic N and soluble P contents in the rhizosphere and nonrhizosphere soil of wheat plants grown in both control and porous-mineral-treated plots. We observed that unlike the amendment with zeolite, the application of diatomite, montmorillonite and bentonite significantly increased the inorganic N content in both rhizosphere and nonrhizosphere soil (Figure 5A). The inorganic N content in the rhizosphere soil from plots treated with diatomite (51.4 mg N kg^{-1}) was significantly higher than that from plots treated with montmorillonite (37.9 mg N kg^{-1}) and bentonite (26.8 mg N kg^{-1}). Similar results were also observed in nonrhizosphere soil. The highest inorganic N content was detected in the soil samples collected from plots treated with diatomite (41.2 mg N kg^{-1}), followed by that in the soil samples collected from plots treated with montmorillonite (29.1 mg N kg^{-1}) and bentonite (25.6 mg N kg^{-1}) (Figure 5A).

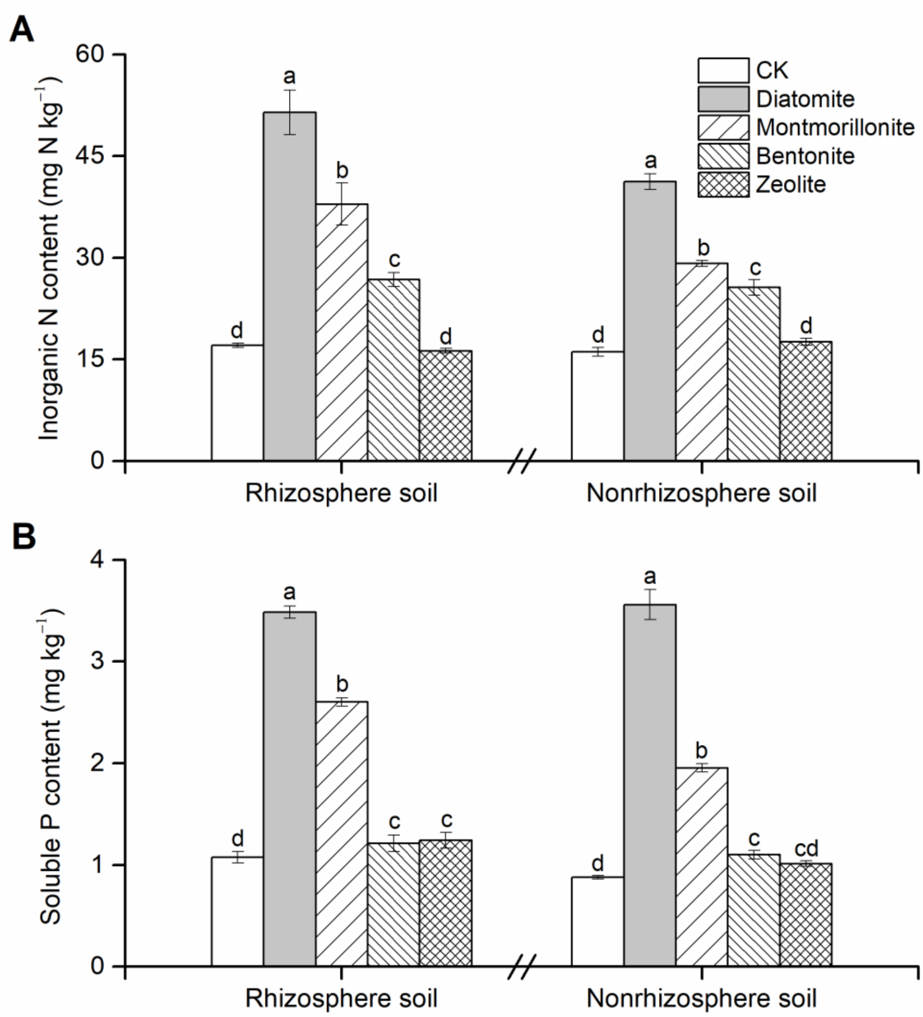

Figure 5. Inorganic N and soluble P content analysis in the rhizosphere and nonrhizosphere soil of wheat plants grown in control (CK) and different porous-mineral-amended plots were examined. (**A**) Inorganic N contents. (**B**) Soluble P contents. Values were means and standard deviations of three replicates (n = 3). Different lowercase letters denote significant difference among different porous-mineral treatments ($p < 0.05$).

The soluble P content was also increased in both rhizosphere and nonrhizosphere soil amended with different porous minerals. In rhizosphere soil, an increase of 224.2%, 142.1%, 12.7% and 15.6% was, respectively, observed in the samples from plots treated with diatomite, montmorillonite, bentonite and zeolite (Figure 5B). A similar increase was also observed in nonrhizosphere soil, except for that from plots treated with zeolite, which showed no significant difference from the control samples. An increase of 305.5%, 122.7% and 25.5% was, respectively, observed in the samples from plots treated with diatomite, montmorillonite and bentonite (Figure 5B).

3.4. Porous Minerals Altered Soil Microbial Abundance and Community Composition

To assess the effects of porous-mineral amendments on soil microbial abundance, we analyzed the copy numbers of 16S and 18S genes in the rhizosphere and nonrhizosphere soil of wheat plants grown in control (CK) and different porous-mineral-amended plots. Compared with that in the control samples, there was a significant increase in 16S rRNA gene copy numbers in the rhizosphere soil of wheat plants from plots amended with diatomite (by 41.1%), bentonite (29.9%) and zeolite (102.4%). However, a remarkable decrease was observed in nonrhizosphere soils amended with diatomite (by 18.8%) and montmorillonite (by 42.8%; Figure 6A). Similarly, 18S rRNA gene copy numbers significantly increased in the rhizosphere soil from plots amended with diatomite (by 209.6%), montmorillonite (by 89.2%), bentonite (by 146.8%) and zeolite (by 175.9%), which was in contrast with the decrease in the nonrhizosphere soil from plots amended with diatomite (by 37.1%), montmorillonite (by 49.3%) and zeolite (by 13.0%; Figure 6B). Therefore, the application of porous minerals under salt stress increased soil microbial abundance in the rhizosphere of wheat plants.

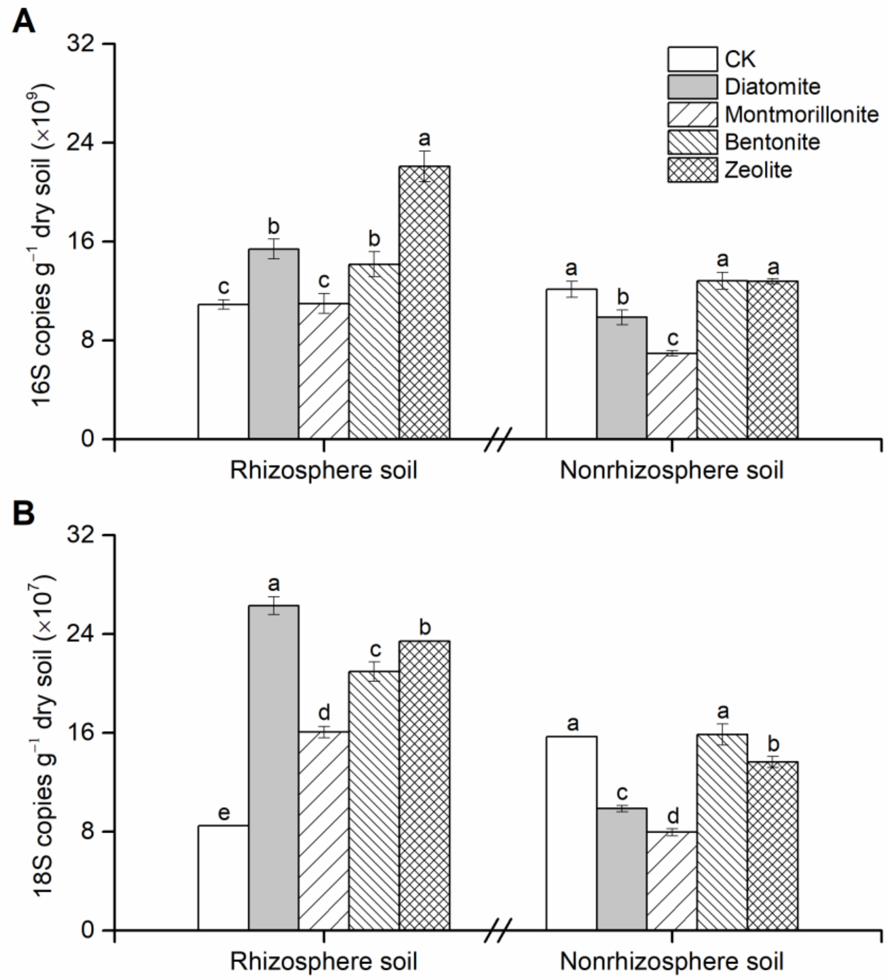

Figure 6. Soil microbial abundance analysis in the rhizosphere and nonrhizosphere of wheat plants grown in control (CK) and different porous-mineral-amended plots. (**A**) 16S rRNA gene copy numbers. (**B**) 18S rRNA gene copy numbers. Values are means and standard deviations of three replicates (n = 3). Different lowercase letters denote significant difference among different porous-mineral treatments ($p < 0.05$).

To decipher the effects of porous-mineral application on soil microbial community composition in the rhizosphere and nonrhizosphere of wheat plants, we carried out high-throughput sequencing analysis. A total 374,737 high-quality 16S rRNA gene sequences clustered into 4780 bacterial OTUs representing 40 phyla were obtained. The top 10 most abundant phyla were *Proteobacteria*, *Actinobacteriota*, *Acidobacteriota*, *Gemmatimonadota*, *Chloroflexi*, *Bacteroidota*, *Myxococcota*, *Verrucomicrobiota*, *Desulfobacterota* and *Firmicutes*, which accounted for 95.8–96.6% of the total bacterial taxa (Figure 7A,B).

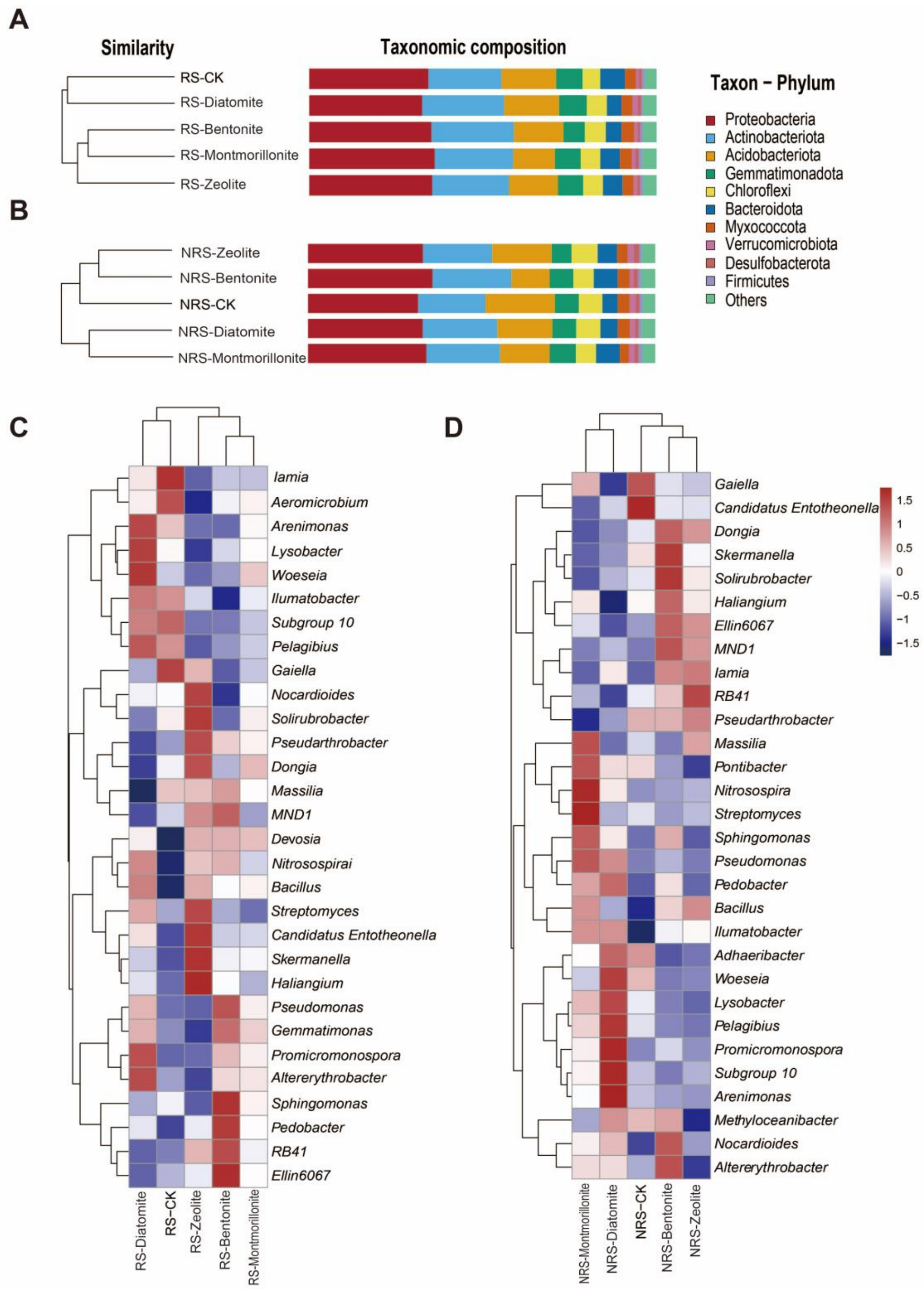

Figure 7. Soil microbial community analysis in the rhizosphere and nonrhizosphere of wheat plants grown in control (CK) and different porous-mineral-amended plots. (**A**,**B**) Hierarchical clustering diagrams based on Bray–Curtis similarity at phylum levels. (**C**,**D**) Heat maps of the top 30 bacteria at genus levels. RS, rhizosphere soil; NRS, nonrhizosphere soil.

The amendment of porous minerals significantly shifted the composition of the soil bacterial community in both the rhizosphere and nonrhizophere of wheat plants. The relative abundances of specific taxa in rhizosphere soils from plots amended with zeolite and bentonite significantly increased at the phylum level, such as *Firmicutes* (by 71.4% and 72%, respectively), *Entotheonellaeota* (by 169% and 38%, respectively), *Dependentiae* (by 100% and 167%, respectively), *Bdellovibrionota* (by 8.5% and 25.8%, respectively), *Patescibacteria* (by 23.7% and 39.1%, respectively) and *Elusimicrobiota* (by 15.3% and 25.2%, respectively). This pattern was contradictory to the decrease in other taxa, such as *Hydrogenedentes* (by 37.3% and 62.4%, respectively), *Fibrobacterota* (by 10.7% and 47.8%, respectively), *Planctomycetota* (by 11.7% and 35.6%, respectively), *Latescibacterota* (by 47.8% and 49.2%, respectively), *Methylomirabilota* (by 25.7% and 28.6%, respectively), *Desulfobacterota* (by 29% and 42.5%, respectively) and *Verrucomicrobiota* (by 29.4% and 12.2%, respectively) (Figure 7A). In the nonrhizosphere soils from plots amended with different porous minerals, both *Gemmatimonadota* and *Firmicutes* increased in relative abundance (by 19.5–32.2% and 15.1–51.8%, respectively), which was contrasted with the decrease in *Chloroflexi* (by 7.1–22.3%), *Desulfobacterota* (by 16.9–38.2%), *Entotheonellaeota* (by 20.5–34.3%) and *Bdellovibrionota* (by 9.3–29.7%) (Figure 7B).

At genus level, in rhizosphere soil, zeolite amendment increased the relative abundances of *Pseudarthrobacter* (by 215.0%), *Nocardioides* (by 50.9%) and *Nitrosospira* (by 60.2%), with decreased *Ilumatobacter* (by 19.3%), *Lysobacter* (by 54.6%), *Thermomonas* (by 66.6%), *Thioalkalispira-Sulfurivermis* (by 84.6%) and *Thiobacillus* (by 100.0%). Bentonite amendment increased the relative abundances of *Sphingomonas* (by 12.4%), *Pseudarthrobacter* (by 35.5%), *Promicromonospora* (by 36.1%) and *Nitrosospira* (by 39.4%), with decreased *Lysobacter* (by 13.1%) and *Nocardioides* (by 17.1%). Diatomite amendment decreased *Massilia* and *Pseudarthrobacter* (by 45.4% and 21.0%, respectively) and increased *Promicromonospora*, *Lysobacter* and *Pseudomonas* (by 95.4%, 56.7% and 56.1%, respectively) (Figure 7C). The relative abundances of *Sphingomonas*, *Promicromonospora*, *Pontibacter*, *MND1*, *Devosia* and *Adhaeribacter* in nonrhizosphere soil was significantly lower than those in rhizosphere soil (Figure 7D).

To explore the relationship between soil bacterial communities and environmental factors in different porous-mineral treatments, we performed CCA analysis. Approximately 31.3% and 20.4% of the total variation in bacterial community structure was explained by the two canonical axes, respectively (Figure S1). This suggested that soil bacterial community structure was in close association with environmental factors, especially with soil EC ($p < 0.01$), p content ($p< 0.01$), Na^+ content ($p < 0.01$), Mg^{2+} content ($p < 0.01$), SAR ($p < 0.01$), K^+/Na^+ ratio ($p < 0.01$) and N content ($p < 0.01$).

4. Discussion

4.1. The Resistance of Wheat Plants to Saline Stress Was Promoted by Porous Minerals

Similar to other soil amendments, the application of these porous minerals significantly increased the growth of wheat plants, as indicated by the increased fresh mass at both the stem elongation and maturity stages (Figure 1A–D and Figure 2A–C) [30]. The application of bentonite or zeolite also significantly increased the grain yield of wheat plants at the maturity stage (Figure 2E–I). The increased grain yield of wheat plants grown in plots amended with bentonite or zeolite was due to both the increased ear grain number and grain size (Figure 2H,I). The reasons behind this behavior could be probably attributed to the ameliorated soil properties and microbial community that resulted from the application of porous minerals in coastal saline land.

4.2. Application of Porous Minerals Ameliorated Soil Properties in Coastal Saline Land

To understand how porous-mineral application promoted wheat growth and seed production, we compared the soil properties in the rhizosphere and nonrhizosphere of wheat plants grown in control and porous-mineral-amended plots. Porous-mineral amendments significantly ameliorated the properties of coastal soil, as indicated by the altered pH value, EC and ion homeostasis (Figure 3A–F and Figure 4A,B). The promoted shoot growth and grain yield of wheat plants could be attributed to the decreased soil salt accumulation. The Na^+ and Mg^{2+} content in the soils collected from the rhizosphere and nonrhizosphere of wheat plants grown in plots amended with bentonite or zeolite was significantly lower than those from the control or diatomite- or montmorillonite-amended plots (Figure 3D,F). This was also supported by the higher soil K^+/Na^+ ratio and lower soil SAR in plots amended with bentonite or zeolite (Figure 4A,B). Compared to other silicate minerals, the spacious porous structure with large channels in bentonite and zeolite could positively affect the exchange capacity of cations (CEC, 200–300 meq 100^{-1} g) and subsequently promote the substitution of ions and reduce the contents of salt [31]. However, a recent study showed that the soil SAR in zeolite-treated soils increased by 65% and 143% [32]. This could be due to the different soil types used in the former studies (sandy loam saline) and this (clay loam saline) study. Similar observations were also reported in a previous study, i.e., that soil amendment with zeolite effectively ameliorated the salinity stress of barley plants and improved the nutrient balance in sandy soil [33]. Bentonite can absorb hydrated cations (e.g., K^+, Na^+, Mg^{2+}) with an ion exchange capacity reaching 60–150 meq 100 g^{-1} [12]. Diatomite also has a porous structure and high surface area [34]. However, its Na^+ content and SAR value were significantly higher than other clay minerals (Figures 3D and 4B). This could be mainly ascribed to the lower cation exchange capacity (CEC) of diatomite than bentonite and zeolite [35]. The discrepancy in the effects of different porous minerals on wheat shoot growth and grain yield could be potentially related to their variant physico-chemical properties (Table 1). Zeolite amendment was more conducive to shoot growth and seed production than other treatments, probably due to the greater reduction in soil salinity, whereas the positive effects of bentonite might also be attributed to the higher total N and soil organic matter of itself (Figure 3D; Table 1).

4.3. Soil Nutrients Were Improved in Coastal Saline Land Amended with Porous Minerals

It is well documented that porous minerals play a dominant role in the enhancement of soil nutrient usage efficiency [9,36]. To further explain why the growth and grain production of wheat plants grown in plots amended with porous minerals were increased in coastal saline land, we examined the nutrients of rhizosphere and nonrhizosphere soil. The application of diatomite, montmorillonite and bentonite all significantly increased the inorganic N content in both rhizosphere and nonrhizosphere soil (Figure 5A). The soluble P content in both rhizosphere and nonrhizosphere soil amended with different porous minerals was also significantly higher (Figure 5B). These observations were consistent with previous reports that porous minerals affected soil physical, chemical and biological properties, thus enhancing nutrient uptake and crop growth [1,3].

Since soil salinity could severely affect crop productivity, a significantly positive correlation (r = 0.7, $p < 0.01$) between plant height and fresh mass was also observed (Table S1). The fresh mass of wheat plants at the stem elongation stage was significantly negatively related to Na^+ content (r = −0.5 and −0.6, $p < 0.05$) and SAR (r = −0.5, $p < 0.05$; r = −0.7, $p < 0.01$), but positively related to K^+/Na^+ ratio (r = 0.7 and 0.7, $p < 0.01$) in both rhizosphere and nonrhizosphere soil (Tables S1 and S2). The increased inorganic N and soluble P content in both rhizosphere and nonrhizosphere soil could be owing to the adsorption of nutrient ions to the porous structure of these minerals, which slowed the release of nutrients [37–39]. Indeed, zeolite could improve the usage efficiency of N by reducing NH_3 volatilization [10]. In both rhizosphere and nonrhizosphere soil, no significant difference in inorganic N content was observed between control and zeolite-amended plots (Figure 5A). This could be explained by the higher N usage due to the promoted wheat growth and seed production.

4.4. Porous-Mineral Amendments Shaped Rhizosphere Soil Microbial Communities under Salt Stress

Microbial populations play an instrumental role in maintaining the stability of agroecosystems [40]. In coastal saline areas, crop yield was severely affected by nutrient deficiency and microbial depletion [30], as soil salinity affected both soil microbial community structure and activities [41,42]. Soil microbial communities were also shaped by other environmental factors in their habitats [36]. The addition of porous minerals prominently affected the soil properties in the tested plots, which would inevitably influence the soil microbial community structure. Based on the analysis of 16S and 18S rRNA gene copy numbers, we found that the application of porous minerals (excluding montmorillonite) significantly increased the abundance of bacteria and fungi in rhizosphere soil (Figure 6A,B). A positive correlation between the abundance of bacteria and soil pH value (r = 0.7, $p < 0.01$), and between the abundance of fungi and EC (r = 0.6, $p < 0.05$), Mg^{2+} (r = 0.5, $p < 0.05$), and inorganic N (r = 0.7, $p < 0.01$) and soluble P (r = 0.5, $p < 0.05$), was observed in rhizosphere soil (Table S1), which is consistent with the results of previous reports [43,44].

The effects of the same kind of porous mineral on the abundance of both bacteria and fungi were different between rhizosphere and nonrhizosphere soils (Figure 6A,B). The positive relationship between plant fresh mass and bacterial abundance in rhizosphere soil (r = 0.8, $p < 0.01$) implied that plant input in soil from increased biomass affected the bacterial community, and in turn, the bacterial community promoted plant growth (Table S1). Soil environmental factors also exhibited distinct effects on the abundance of both bacteria and fungi between rhizosphere and nonrhizosphere soil, which is in accordance with previous studies (Tables S1 and S2) [45–47]. These results could be attributed to the prominent difference of physicochemical properties driving niche differentiation [48,49].

Bacterial communities could be influenced by the minerals in their living microhabitats, especially at low concentration in soil [50,51]. High bacterial diversity facilitated plants to coabsorb nutrient elements and promote further growth of plants [52]. Here, *α-, γ-proteobacteria*, *Actinobacteria*, *Vicinamibacteria* and *Acidimicrobiia* were detected as the predominant bacterial phyla in our research samples, which mirrored the results of a previous study [53]. Our CCA results provided strong evidence that porous-mineral amendment shifted bacterial community structures by altering soil properties in coastal saline land [54]. At the genus level, the application of zeolite and bentonite led to the enrichment of *Pseudarthrobacter*, *Nocardioides, Sphingomonas* and *Promicromonospora*, which is associated with chemoheterotrophy, fermentation, N fixation, chloroplasts and photoautotrophy (Figure 7C,D). Hence, our discoveries are consistent with previous research that minerals may help plants recruit plant-growth-promoting rhizobacteria (PGPRs) from soil and enhance the tolerance of plants to salt stress [13,55].

5. Conclusions

In summary, soil amendment with porous minerals significantly enhanced the salt resistance of wheat plants in coastal saline land, resulting in a 14.8~61.2% increase in plant fresh mass, 3.8~58.8% increase in seed size and 1.4~57.5% increase in seed number. Compared with diatomite, montmorillonite and bentonite, zeolite was the most efficient mineral amendment in the improvement of wheat fresh mass and grain production. Porous-mineral amendment decreased soil Na^+ content and SAR, and increased soil nutrients and the abundance of bacterial 16S rRNA and fungal 18S rRNA. The increase in shoot growth and grain yield occurred most likely due to the remarkably decreased Na^+ content and SAR, as well as the increased soil microbial abundance and community composition. The findings in our study will provide important guidance for salt-affected soil remediation with porous minerals in coastal saline areas. Future study on the effects of the application of these porous minerals, together with other fertilizer, in high-salinity soils will be carried out to assess their potential in agricultural production.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/agronomy13092380/s1, Figure S1: Canonical correspondence analysis (CCA) of bacterial community composition based on Bray–Curtis similarity. RS: rhizosphere soil; NRS: nonrhizosphere soil; Moisture, soil moisture content; pH, soil pH value; EC, electrical conductivity; K, K^+ content; Na, Na^+ content; Ca, Ca^{2+} content; Mg, Mg^{2+} content; K/Na, K^+/Na^+ ratio; SAR, sodium adsorption ratio; N, inorganic nitrogen content; P, soluble phosphorus content; Table S1: Correlation matrix of plant morphology and soil physicochemical property in the rhizosphere of wheat plants; Table S2: Correlation matrix of plant morphology and soil physicochemical property in the nonrhizosphere of wheat plants.

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