Science of the Total Environment 842 (2022) 156952

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Integrated organic and inorganic fertilization and reduced irrigation altered prokaryotic microbial community and diversity in different compartments of wheat root zone contributing to improved nitrogen uptake and wheat yield

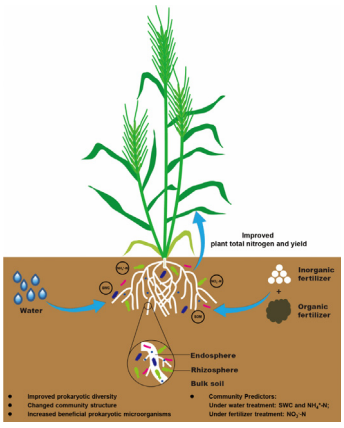
Chao Wang [a], Haiyang Ma [a,d], Zhihan Feng [b], Zhenxing Yan [a], Bolong Song [a], Jialong Wang [b], Yuyin Zheng [b], Weiping Hao [a], Wenying Zhang [c,*], Minjie Yao [b,*], Yaosheng Wang [a,*]

[a] Institute of Environment and Sustainable Development in Agriculture, Chinese Academy of Agricultural Sciences, Beijing 100081, China
[b] Engineering Research Center of Soil Remediation of Fujian Province University, College of Resources and Environment, Fujian Agriculture and Forestry University, Fuzhou 350002, China
[c] Institute of Dryland Farming, Hebei Academy of Agriculture and Forestry Sciences, Hengshui 053000, China
[d] Key Laboratory of Tropical Crops Nutrition of Hainan Province, South Subtropical Crops Research Institute, Chinese Academy of Tropical Agricultural Sciences, Zhanjiang 524091, China

HIGHLIGHTS

- Water regimes more drastically affected the prokaryotic structure and diversity.
- Increased water and organic fertilizers improved beneficial prokaryotic microbes.
- SWC and NH_4^+-N were key predictors of prokaryotic composition under water treatments.
- NO_3^--N was the key predictor of prokaryotic composition under fertilizer treatments.
- Water and fertilization promoted N uptake and yield by altering prokaryotic microbes.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Abasiofiok Mark Ibekwe

Keywords:
Physicochemical factors
Prokaryotic microorganisms
Bulk soil
Rhizosphere
Endosphere
Yield

ABSTRACT

The effect of long-term water and integrated fertilization on prokaryotic microorganisms and their regulation for crop nutrient uptake remains unknown. Therefore, the impact of soil water and integrated fertilization after eight years on prokaryotic microbial communities in different compartments of root zone and their association with wheat nitrogen (N) absorption and yield were investigated. The results showed that compared with fertilization treatments (F), water regimes (W) more drastically modulated the prokaryotic microbial community structure and diversity in bulk soil, rhizosphere and endosphere. The increase of irrigation improved the prokaryotic diversity in the rhizosphere and endosphere while decreased the diversity in the bulk soil. Application of organic fertilizers significantly improved soil organic matter (SOM) and nutrient contents, increased rhizosphere and endophytic prokaryotic microbial diversity, and elevated the relative abundance of aerobic ammonia oxidation and nitrification-related functional microorganisms in rhizosphere and endosphere. Increasing irrigation elevated the relative abundance of functional microorganisms related to aerobic ammonia oxidation and nitrification in the rhizosphere and endosphere. Soil water content (SWC) and NH_4^+-N as well as NO_3^--N were key predictors of prokaryotic microbial community

* Corresponding authors.
E-mail addresses: zxm.0223@163.com (W. Zhang), yaomj@fafu.edu.cn (M. Yao), wangyaosheng@caas.cn (Y. Wang).

http://dx.doi.org/10.1016/j.scitotenv.2022.156952
Received 28 April 2022; Received in revised form 18 June 2022; Accepted 20 June 2022
Available online 22 June 2022

composition under W and F treatments, respectively. Appropriate application of irrigation and organic fertilizers increased the relative abundance of some beneficial bacteria such as *Flavobacterium*. Water and fertilization treatments regulated the prokaryotic microbial communities of bulk soil, rhizosphere and endosphere by altering SWC and SOM, and provided evidence for the modulation of prokaryotic microorganisms to promote nitrogen uptake and wheat yield under long-term irrigation and fertilization. Conclusively, the addition of organic manure (50 %) with inorganic fertilizers (50 %) and reduced amount of irrigation (pre-sowing and jointing-period irrigation) decreased the application amount of chemical fertilizers and water, while increased SOM and nutrient content, improved prokaryotic diversity, and changed prokaryotic microbial community structure in the wheat root zone, resulting in enhanced nutrient uptake and wheat yield.

1. Introduction

Water and fertilizer are the two most important factors affecting crop growth and productivity. Some major grain producing regions, such as the North China Plain, have insufficient groundwater and are facing serious fresh water resource crisis (Dikgwatlhe et al., 2014). Furthermore, the extensive application of inorganic fertilizers has caused the degradation of ecosystem structure and functions, including soil acidification, reduction in nutrient availability, loss of biodiversity and environmental pollution (Tilman et al., 2002; Guo et al., 2010; Sebilo et al., 2013; Zhou et al., 2015; Chen et al., 2018). The reduction in the use of chemical fertilizers and the integrated application of organic and inorganic fertilizers are important measures for sustainable agricultural development (Liu et al., 2021). Previous studies have shown that application of organic fertilizers not only increases soil fertility including soil carbon and nitrogen (N), but also improves the content of quick-acting nutrients such as soil nitrate and ammonium (Qaswar et al., 2020). In addition, organic fertilizers can reduce nutrient leaching in the soil and enhance soil fertility retention capacity (Bei et al., 2018). Therefore, effective management strategies e.g., integrated fertilization strategies, must be formulated to improve the efficiency of water and fertilizers in order to ensure sustainable development of agriculture (Quemada and Gabriel, 2016).

Microbial community is an important part of soil ecosystem and plays an important role in maintaining soil ecological function. It directly participates in nutrient cycle, energy flow and organic matter degradation (Chen et al., 2017). As an important index for evaluating soil quality, soil microorganisms are significantly affected by agricultural management measures such as irrigation and fertilization (Frenk et al., 2014; Feng et al., 2015). Reduction in soil water content can limit soil extracellular enzyme and microbial activity, thereby affecting soil microbial diversity (Henry, 2012; Moyano et al., 2013; Wang et al., 2015; Preece et al., 2019). Similarly, water shortage can reduce soil organic carbon content and affect the structure of soil microbial community (Bastida et al., 2017). Yang et al. (2018b) found that compared with the non-irrigation treatment, irrigation together with chemical or organic fertilization significantly increased the number of bacteria while considerably decreased the relative abundances of Actinobacteria and Saccharibacteria. Bai et al. (2019) noted that prokaryotic microbial richness and evenness increased with soil water content, and changes in community composition were significantly affected by soil relative water content. Nevertheless, the responses of prokaryotic microbial community in bulk soil, rhizosphere and endosphere to irrigation regimes have not been systematically investigated.

Organic fertilizer is rich in nutrients such as organic matter, humus and beneficial microorganisms (Corato, 2020). The application of organic fertilizers can increase the abundance of soil microorganisms and benefit the functional diversity of soil microorganisms (Orr et al., 2012; Jannoura et al., 2014; Ling et al., 2014; Cui et al., 2018; Kumar et al., 2018). Moreover, it can also adjust the microbial community structure and improve the soil micro-ecological environment (Igalavithana et al., 2017; Cui et al., 2018; Ikoyi et al., 2020). Shen et al. (2010) found that the application of organic fertilizers for 20 years caused changes in bacterial community composition of acid soils in Northeast China. Wang et al. (2017) reported that application of organic fertilizers increased the abundance of commensal bacteria such as Proteobacteria. Cui et al. (2018) noted that the abundance of Proteobacteria and Chloroflexi in the soil increased after adding organic fertilizers. Organic fertilizers promote the formation of special microbial functional groups in the soil, such as groups related to nitrogen mineralization, ammonification and nitrification (Ouyang et al., 2018). These functional groups participate in the degradation of complex organic compounds in the soil (Hartmann et al., 2015; Davide et al., 2016), facilitate the decomposition of organic matter in the soil and the soil nutrient cycle, increase the concentration of available nutrients for crops, and form a benign soil nutrient cycle (Li et al., 2017). However, the gaps for the impact of long-term organic fertilization on prokaryotic microbial community in bulk soil, rhizosphere and endosphere still exist.

It was reported that in soils where only inorganic fertilizers and especially nitrogen fertilizers were applied, nitrogen application itself did not have a significant negative impact on soil prokaryotic microorganisms in agricultural systems. When nitrogen application reduced soil pH, soil prokaryotic microorganism biomass, activity and community composition were indeed affected (Geisseler and Scow, 2014). Ramirez et al. (2010) found that increased nitrogen addition did not have consistent effects on bacterial community richness and diversity, while bacterial diversity was negatively correlated with fertilization ratio. However, some studies showed that long-term application of inorganic fertilizers reduced soil bacterial richness and diversity (Hu et al., 2018; Wang et al., 2018c). The tendency of inorganic fertilizers to reduce bacterial abundance and diversity was also found under short-term fertilization condition (Guo et al., 2018). On the contrary, Tosi et al. (2021) reported that nitrogen input had little effect on soil prokaryotic microorganism community structure, and 10-year nitrogen input was positively correlated with bacterial biomass. Other studies have shown that in the soil environment where only inorganic fertilizers were applied, the soil microbial population structure was scattered, and most of them were some general-purpose oligotrophic microorganisms such as Acidobacteria (Hartmann et al., 2015; Davide et al., 2016). Wang et al. (2017) found that application of inorganic fertilizers increased the abundance of Bacteroidetes and Acidobacteria. Zhang et al. (2019) observed that after short-term N addition, the content and element ratio of soil organic carbon (SOC) and total nitrogen (TN) changed, and the microbial community distribution was restricted by N addition. When organic fertilizers are applied, previous studies have shown that long-term inorganic and organic fertilization significantly changed soil bacterial diversity and communities in rice fields (Ding et al., 2016) and wheat-rice rotation fields (Tian and Niu, 2015). Likewise, Ji et al. (2018) reported that with the increase of organic fertilizer application ratio, soil bacterial diversity increased and community structure changed significantly. They also found that Proteobacteria had higher relative abundance in fertilization treatments that increased with the elevation of organic fertilizer application ratio, whereas Actinobacteria did the opposite. Wu et al. (2020) found that fertilization changed the abundance and diversity of bacteria in the rhizosphere soil of crops, and the relative abundances of *Nitrospira*, *Pseudomonas*, *Arthrobacter* and *Bacillus* were significantly elevated by increasing the application of organic fertilizers and reducing the application of chemical fertilizers for two consecutive years. Ye et al. (2019) noted that the combined application of organic and inorganic fertilizers increased soil pH and organic carbon content, and improved prokaryotic microbial diversity and community structure after 27 years of fertilization. Wang et al. (2018b) found that in long-term fertilization of black soil in Northeast China, soil NH_4^+, TN and TC explained 21 %, 19 % and 18 % of the urea-decomposing microbial abundance variations among different organic and inorganic fertilizer treatments, respectively, and they also proposed that organic fertilizer

application was the main driver of the changes of urea-decomposing microbial community. Nonetheless, long-term impact of organic or integrated fertilization on soil prokaryotic microorganisms in different compartments compared with chemical fertilizer application is still unclear.

Crops are closely related to the broad-spectrum microbiota in the rhizosphere and endosphere, and those microbiota are collectively referred to as crop microbiota (Liu et al., 2017; Liu and Brettell, 2019; Zhang et al., 2019). They can improve crop nutrient access, stress tolerance and crop productivity while inhibit pathogens (Sessitsch and Mitter, 2015; Qiu et al., 2019; Chen et al., 2020; Trivedi et al., 2020). Multiple studies have shown that the composition of microbial community varies by plant compartments (for example, leaf phyllosphere, rhizosphere and endosphere), and may respond differently to fertilization (Tkacz et al., 2020; Trivedi et al., 2020). During plant growth, changes in plant immune system activity may also have a greater impact on microbial changes in the endosphere and root surface than on the rhizosphere (Edwards et al., 2018). Currently, the impact of water and integrated inorganic and organic fertilization on prokaryotic microbial diversity and community composition and their association with nutrient absorption and crop yield still remain unknown. Therefore, this study aimed to investigate and unravel the mechanisms for the changes of prokaryotic microbial communities in the three compartments (bulk soil, rhizosphere and endosphere), nutrient uptake and yield of wheat plants under long-term water and fertilization strategies.

2. Materials and methods

2.1. Experimental description and soil sampling

The experiment site was located at the Institute of Dryland Farming, Hebei Academy of Agriculture and Forestry Sciences in North China Plain (37°54′37″ N, 115°42′53″ E). The soil type of the experiment site is Ochri-Aquic Cambosols. The multi-year average temperature in this area is 12.8 °C and the annual average precipitation is about 497.0 mm with uneven seasonal and inter-annual distribution. The average precipitation during the multi-year growth period of winter wheat is 120–160 mm. The average temperature and precipitation during the wheat growth period of 2019 and 2020 were 10.9 °C and 13.1 mm, respectively. The average temperature and precipitation in each month during the wheat growth period were shown in Table S1.

In 2012, the long-term irrigation and fertilization field experiment of wheat was initiated. The experiment was arranged in a split-plot design. The main plots were four irrigation regimes, and the subplots were four fertilization types with three replicates in each treatment. The size of each experimental plot was 17.4 × 10 m^2, with 80 cm isolation zone between the plots, and a 2 m deep plastic film was used to prevent seepage between the adjacent plots. Four irrigation treatments included (1) the plots were irrigated thrice during the growth period at 120 mm before sowing, 80 mm at the jointing growth stage and 80 mm at the flowering growth stage (W3), (2) the plots were irrigated twice during the growth period at 120 mm before sowing and 80 mm at the jointing growth stage (W2), (3) the plots were irrigation once at 120 mm before sowing (W1), (4) the plots were not irrigated during the whole period (W0). Four fertilization treatments under each irrigation treatment comprised (1) organic fertilization with organic N at 270 kg N hm^{-2} (M100), (2) organic fertilization with organic N at 135 kg N hm^{-2} and inorganic N at 135 kg N hm^{-2} (M50), (3) inorganic fertilization at 270 kg N hm^{-2} (M0) and (4) no fertilization (CK). The organic N applied was cow dung containing total carbon of 34.16 %, total N content of 1.14 %, total P content of 1.01 % and total K content of 0.80 %. The urea (46 % N), superphosphate (18 % P_2O_5) and potassium chloride (60 % K_2O) were used as the inorganic N, P and K fertilizers. The 40 % inorganic N, all the organic manure, P and K fertilizers were applied as basal fertilizers before sowing, and 60 % inorganic N fertilizer was applied at the jointing growth stage. The amount of P and K in the cow dung applied each year was determined before fertilization, and the same amount of P and K as in the organic fertilization treatments were applied in the inorganic fertilization treatments by adding inorganic P and K fertilizers. The application amounts of P_2O_5 and K_2O in M50 treatment were 87 kg hm^{-2} and 72 kg hm^{-2}, respectively, and were 174 kg hm^{-2} and 144 kg hm^{-2} in M0 treatment, respectively.

The soil samples were collected after seven days of the last irrigation event at the flowering and grain filling stage in 2020. Three bulk soil samples were collected from each plot using the five-point sampling method. The collected bulk soil samples were divided into two portions for respective soil physiochemical and microbial determination. Three wheat plant samples were collected at each sampling point, and the soil was shaken off the roots. The soil attached to the surface of wheat roots was considered as rhizosphere soil. The roots were cut off with sterilized scissors and placed in sterile bags. All soil and root samples were stored in an ice box and transported back to the laboratory. The soil samples used to determine the physicochemical properties were stored at 4 °C. The soil for microbial measurement and root samples were stored at −20 °C. The plant samples were dried at 70 °C to constant weight and then ground to fine powder for total carbon and nitrogen determination.

2.2. Soil physicochemical properties

The bulk impurities were removed in the fresh soil samples. The soil moisture content (SWC) was determined by the drying method at 105 °C in an oven. Soil pH was measured by a pH electrode (model LE43, Mettler Toledo International Inc., Shanghai, China) with the soil: water ratio of 1:2.5. Fresh soil samples were extracted with 1 M KCl and the ammonium (NH_4^+-N) and nitrate (NO_3^--N) were measured with a flow injection autoanalyzer (FLA star 5000 Analyzer, Foss, Denmark). Soil organic matter (SOM) was determined by potassium dichromate volumetric method. Soil total carbon (STC), total N (STN), plant carbon (PTC) and nitrogen (PTN) concentrations were measured with an elemental analyzer (vario PYRO cube, Elementar Analysen systeme GmbH, Germany).

2.3. DNA extraction, amplicon sequencing and bioinformatic analyses

In order to separate the rhizosphere and endosphere samples, the root sample was put into a 50 mL sterile Falcon tube and was shaken vigorously after adding 40 mL sterile Phosphate Buffered Saline (PBS) solution in the tube. Then the roots were taken out of the Falcon tube, washed with PBS solution 5–6 times to remove the soil attached to the root surface, and stored as a sample of the root endosphere. The Falcon tube was centrifuged and the pellets were collected as a rhizosphere soil sample. All samples were stored at −20 °C for DNA extraction. In this study, there were a total of 48 bulk soil samples, 36 rhizosphere soil samples and 36 root samples (except the no irrigation treatment (W0) where plants rarely survived). The genomic DNA was extracted with MoBio Powersoil™ DNA Extraction Kit (San Diego, CA, USA), and the DNA quality was detected with NanoDrop Spectrophotometer. The extracted DNA was diluted to 20 ng μL^{-1} and stored at −20 °C for the next step.

The prokaryotic 16S rRNA gene was amplified using primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 909R (5′ -CCCCGYCAAT TCMTTTRAGT-3′) (Xu et al., 2020). A unique 12-nucleotide barcode was attached to the 5′-end of the 515F primer to distinguish each sample. The 25 μL PCR reaction system included 1 μL 20 ng μL^{-1} template DNA, 1 μL 10 μM primers, 9.5 μL sterile water and 12.5 μL MasterMix containing Taq DNA polymerase, Mg^{2+}, PCR buffer and dNTPs. The PCR mixture was pre-denatured at 94 °C for 3 min, followed by 28 cycles of amplification (94 °C for 40 s, 57 °C for 60 s and 68 °C for 45 s), and finally extended at 72 °C for 10 min. The purified PCR products of all samples were mixed with equimolar amounts and sequenced with the Illumina NovaSeq sequencer (Illumina, San Diego, CA, USA; 2 × 250 bp paired ends).

The raw data of sequencing was spliced by FLASH software, and the samples were split by FASTX-Toolkit software according to the barcode information. The sample sequences were imported into the QIIME2 (v2019.10) platform for subsequent processing (https://qiime2.org/). Using the DADA2 pipeline for quality control, chimera removal, and noise

reduction (Callahan et al., 2016), differences at the single nucleotide level were used to distinguish different sequences, resulting in 16S amplicon sequencing variants (ASVs, with 100 % similarity of sequences). 16S ASVs were classified and assigned with reference to the SILVA 132 database (http://www.arb-silva.de/download/archive/qiime/) (Quast et al., 2013). A total of 36,276–265,800 ASVs were obtained per sample. For alpha and beta diversity analysis, all samples were randomly rarefied to the same sequence depth of 36,200 ASVs. A phylogenetic tree was constructed in the QIIME2 platform, and a weighted unifrac distance matrix was obtained for beta diversity analysis. All sequences have been deposited in Sequence Read Archive (SRA) of the National Centre for Biotechnology Information (NCBI) with the accession number of PRJNA849427.

2.4. Statistical analyses

All statistical analyses were performed by R v4.0.5 or SAS 9.2 (SAS Institute, NC, USA). The analysis of variance (ANOVA) was performed to detect significant differences under different water and fertilization treatments. The Permutational Analysis of Variance (PERMANOVA) was implemented to test the response of prokaryotic microbial communities to different water and fertilizer treatments. The vegan package was used to analyze alpha diversity of the prokaryotic microbial community (http://cran.r-project.org/web/packages/vegan/index.html), and the variance analysis was applied to examine the significant differences under different water and fertilizer treatments. The weighted unifrac distance matrix at the ASVs level was implemented for principal coordinate analysis (PCoA) to check the beta diversity of three compartments of prokaryotic microorganisms (bulk soil, rhizosphere and endosphere) under different water and fertilizer treatments. The above alpha and beta diversity and species composition were visualized using ggplot2 (https://cran.r-project.org/web/packages/ggplot2/index). An online tool (https://www.bioincloud.tech) was used to perform linear discriminant analysis (LDA) effect size (LEfSe) to determine biomarkers at different compartments under different water and fertilizer treatments. The correlations of alpha diversity, biomarkers with environmental factors were calculated using the R package “psych” (https://cran.r-project.org/src/contrib/Archive/psych/), and visualized using the R package “pheatmap” (https://cran.r-project.org/src/contrib/Archive/pheatmap/). The online tool (http://www.cloud.biomicroclass.com/) FAPROTAX was used to predict the function of prokaryotic microorganisms in different compartments under different water and fertilizer treatments. Structural equation modeling (SEM) was established using the lavaan package (http://lavaan.ugent.be/start.html) to test the direct and indirect effects of irrigation treatments, fertilization treatments, and prokaryotic microorganisms at different sites on wheat nitrogen uptake and wheat yield. The model was further validated with SWC and SOM instead of irrigation and fertilization treatments, respectively. Prokaryotic microorganisms at different compartments were represented using the first axis of the PCoA data. The optimal model was constructed by χ^2 test ($P > 0.05$), the goodness of fit index (GFI > 0.9), the comparative fit index (CFI > 0.9), and the root mean square error of approximation (RMESA < 0.05).

3. Results

3.1. Effects of water and fertilization treatments on soil physicochemical properties, wheat yield and plant nutrients

Soil pH was significantly affected by water (W) and fertilization (F) treatments ($P < 0.05$) (Table S2). With the decrease of irrigation amount, the pH reduced. Soil pH was highest in the CK treatment while lowest in the M0 treatment. Soil water content (SWC) was significantly affected by W treatment and W × F interaction ($P < 0.05$). For soil nutrients, soil organic matter (SOM), soil total carbon (STC) and soil available nitrogen (NO_3^--N and NH_4^+-N) were significantly affected by W, F and W × F interaction ($P < 0.05$). Across the N treatments, STC and NO_3^--N were highest in W0 treatment. Across the W treatments, the concentration of soil nutrients in CK treatment was lowest. SOM, STN and STC decreased with the reduction in organic fertilizer dosage. Soil NO_3^--N decreased with the reduced inorganic fertilizer dosage.

Plant total N (PTN) and wheat yield were significantly affected by W and F ($P < 0.05$) (Fig. 1). Across the F treatments, PTN increased with the decrease of irrigation amount. The yield was highest in W2 while lowest in W1. Across the W treatments, the PTN under inorganic fertilizer treatments (M50 and M0) was significantly higher than that of organic fertilizer (M100) and no fertilizer treatments (CK), whereas the yield under CK treatment was significantly lower than other treatments. The PTN was significantly positively and linearly correlated with the yield (Fig. 1). Plant total carbon (PTC) was significantly affected by F and W × F interaction ($P < 0.05$). PTC in M50 and M0 treatments was significantly higher than those in M100 and CK treatments (Table S2).

3.2. Effects of water and fertilization treatments on the diversity of prokaryotic communities

The alpha diversity of prokaryotic microbial communities in the three compartments was significantly affected by W treatments ($P < 0.05$). The increase of irrigation reduced the alpha diversity of bulk soil, whereas it increased the alpha diversity in the rhizosphere and endosphere (Fig. 2, Table S3). The alpha diversity of rhizosphere and endosphere were significantly affected by F treatments ($P < 0.05$). Compared with M0, the application of organic fertilizers (M100 and M50) increased the alpha diversity of the rhizosphere and endosphere (Fig. 2, Table S3).

PCoA based on weighted UniFrac distances (Fig. 3A) displayed significant differences in the beta diversity of prokaryotic microorganisms in different compartments (PERMANOVA, $P < 0.05$). Prokaryotic microorganisms in each compartment were distinguished under different W and F treatments. The effect of W treatment was significantly greater than the F treatment, especially in rhizosphere, where different W treatments were obviously distinguished. Similarly, PERMANOVA analysis also showed that different W and F treatments significantly influenced prokaryotic microorganism beta diversity ($P < 0.05$), and the effect of W treatment was significantly greater than the F treatment (Fig. 3).

3.3. Effects of water and fertilization treatments on the composition of prokaryotic communities

The relative abundance of prokaryotic microbial community composition in different wheat compartments shifted significantly across the W and F treatments at phylum level (Figs. 4, S1), and most of them were significantly affected by W, F and W × F interaction ($P < 0.05$, Table S4). In bulk soil, increased irrigation elevated the relative abundance of Proteobacteria, Bacteroidetes, Thaumarchaeota and Verrucomicrobia, while decreased the relative abundance of Actinobacteria, Acidobacteria, Gemmatimonadetes and Planctomycetes. The relative abundance of Proteobacteria, Chloroflexi and Firmicutes increased with the application of organic fertilizers. In the rhizosphere, increasing irrigation improved the relative abundances of Acidobacteria, Chloroflexi, Gemmatimonadetes, Planctomycetes and Verrucomicrobia, while decreased the relative abundances of Actinobacteria, Bacteroidetes and Firmicutes. The relative abundance of Thaumarchaeota and Chloroflexi increased with the application of organic fertilizers. In the endosphere, increasing irrigation augmented the relative abundance of Bacteroidetes and Verrucomicrobia, while decreased the relative abundance of Proteobacteria and Firmicutes. Application of organic fertilizers increased the relative abundance of Gemmatimonadetes and Firmicutes.

The relative abundance of prokaryotic microbial community composition in wheat compartments varied significantly at the genus level between W and F treatments (Figs. S2, S3). The main microbial groups at genus level significantly affected by W and F in the three compartments were determined by LEfSe analysis (Fig. S4). Prokaryotic microorganisms in three compartments were more resistant to F treatments, and the biomarkers

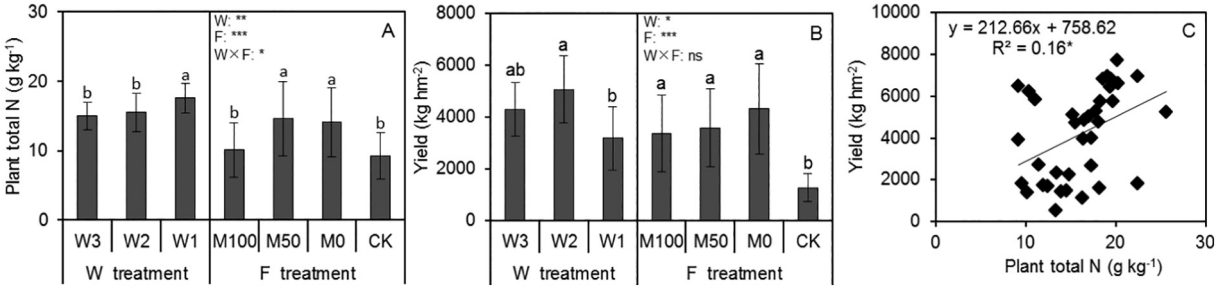


Fig. 1. Effects of different water and fertilizer treatments on plant total N, wheat yield and their relationship. Different letters above the columns indicate significant differences among the treatments according to Duncan's multiple range test at $P < 0.05$. W, F and W × F represent water treatment, fertilization treatment and their interaction, respectively. *, **, *** and ns represent $P < 0.05$, $P < 0.01$, $P < 0.001$ and no significance, respectively.

identified under F treatments were less than W treatments. Among the three compartments, W1 treatment had the most biomarkers. In rhizosphere and endosphere, the number of biomarkers in M0 treatment was more than that in other F treatments (Fig. S4). Four beneficial prokaryotic microorganisms were identified in genus level biomarkers (Fig. 5). In bulk soil, *Flavobacterium*, *Bacillus* and *Stenotrophomonas* were significantly affected by W treatments, and increasing irrigation elevated their relative abundance. In the rhizosphere and endosphere, increasing irrigation significantly decreased the relative abundance of *Bacillus*, *Stenotrophomonas* and *Pseudomonas*. The application of organic fertilizers (M50) considerably increased the relative abundance of *Flavobacterium* in the three compartments (Fig. 5, Table S5).

3.4. Effects of environmental factors on prokaryotic microorganisms

The diversity of prokaryotic microorganisms in different compartments responded differently to environmental factors. The beta diversity of bulk soil was significantly negatively correlated with STN and STC. However, SWC, SOM, STN and STC were significantly positively associated with the alpha diversity of the rhizosphere while remarkably negatively correlated with the beta diversity. Observed richness of endosphere was significantly positively related with SWC, pH and STC. Phylogenetic diversity was significantly positively correlated with STN and STC. The alpha diversity of the endosphere was significantly negatively associated with NO_3^--N. The beta diversity of endosphere was significantly positively related with NO_3^--N

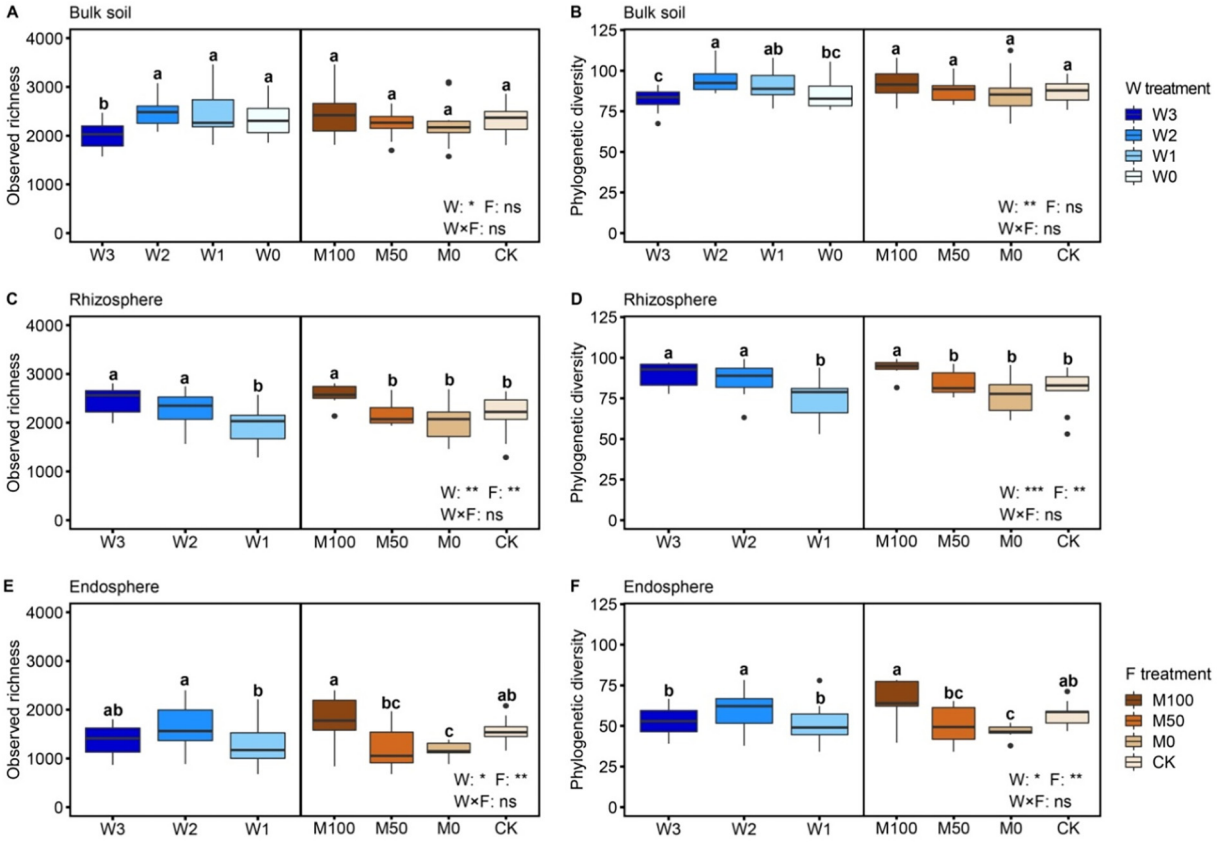


Fig. 2. Effects of different water and fertilizer treatments on alpha diversity of prokaryotic microorganisms in bulk soil, rhizosphere and endosphere. W, F and W × F represent water treatment, fertilization treatment and their interaction, respectively. Different letters indicate significant differences among the treatments according to Duncan's multiple range test ($P < 0.05$). *, **, *** and ns denote $P < 0.05$, $P < 0.01$, $P < 0.001$ and no significance, respectively.

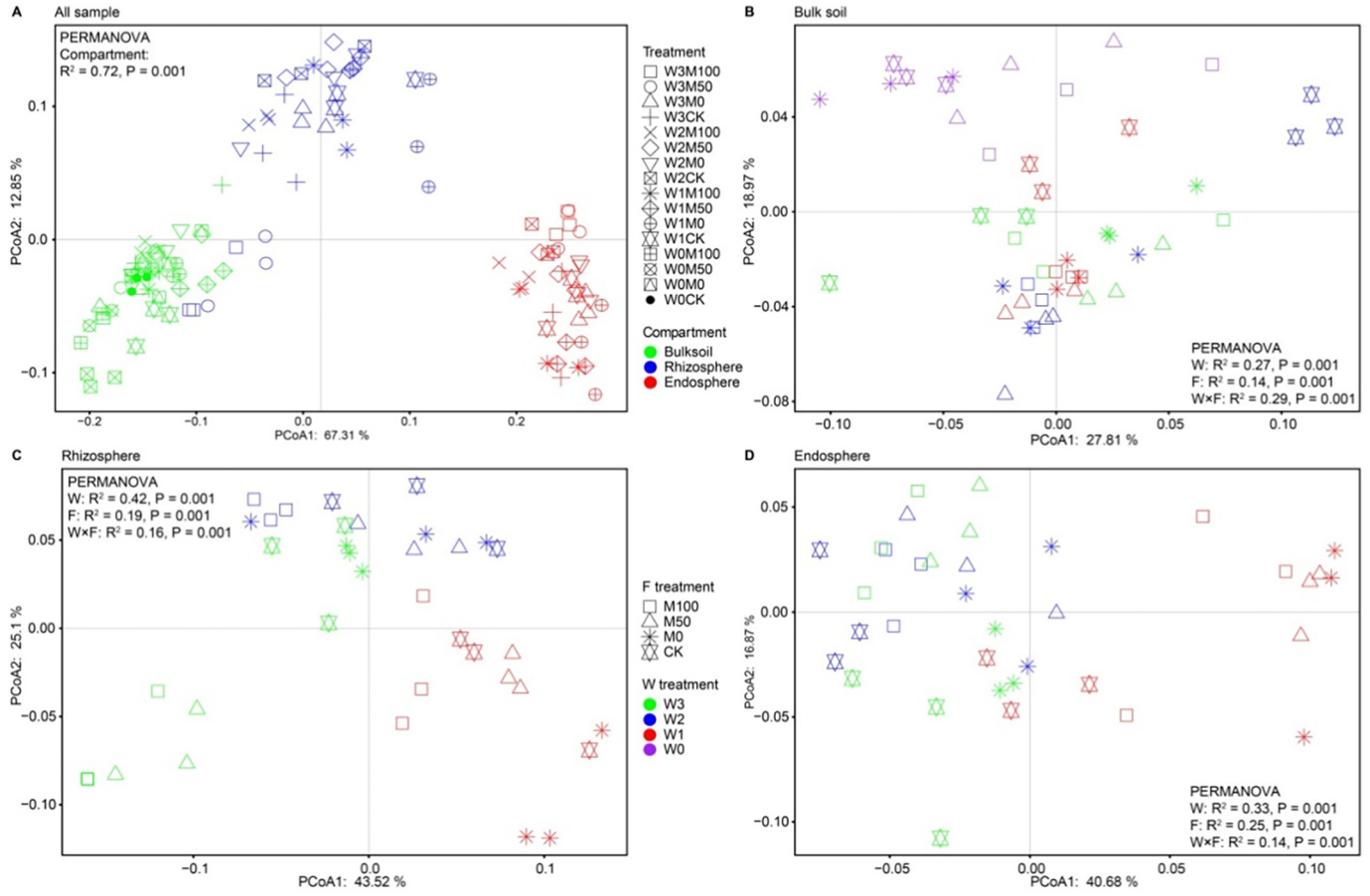


Fig. 3. Effects of different water and fertilization treatments on beta diversity of prokaryotic microorganisms in bulk soil, rhizosphere and endosphere. Principal coordinate analysis was based on weighted UniFrac distances.

and NH_4^+-N while markedly negatively correlated with SWC, pH and STC (Fig. 6A). Spearman correlation analysis was performed to further characterize the relationship between biomarkers and environmental factors under different W and F treatments (Fig. 6B, C). The biomarkers enriched in inorganic fertilizer treatments (M0 and M50) were positively correlated with NO_3^--N, whereas biomarkers enriched in CK and M100 treatments were negatively associated with NO_3^--N (Fig. 6B). Most of the biomarkers enriched in M0 treatment were significantly negatively ($P < 0.05$) correlated with soil pH. Almost all the biomarkers enriched in the CK treatment were significantly negatively associated with SOM, NO_3^--N and STN ($P < 0.05$) while positively correlated with soil pH ($P < 0.05$). In addition, the biomarkers enriched in M0 treatment of rhizosphere were negatively related with SWC, SOM, STN and STC. The biomarkers enriched in M100 (rhizosphere) and M50 (endosphere) treatments were significantly positively correlated with SOM, STN and STC ($P < 0.05$, Fig. 6B).

Most biomarkers enriched in W treatments were significantly correlated with SWC ($P < 0.05$). The biomarkers enriched in W1 treatment were negatively associated with SWC. In contrast, the biomarkers enriched in W2 and W3 treatments were positively related with SWC (except *Pseudomonas*). Nevertheless, the biomarkers enriched in W1 treatment were positively correlated with NH_4^+-N, whereas the biomarkers enriched in W2 and W3 treatments were negatively associated with NH_4^+-N (except *Pseudomonas*). In addition, biomarkers in bulk soil and rhizosphere enriched in W1 treatment were negatively related with STN and STC (Fig. 6C). In summary, most biomarkers were significantly correlated with the environmental factors, indicating that long-term W and F treatments changed the composition of microbial community in wheat root zone.

3.5. Effect of water and fertilization treatments on functional characteristics

FAPROTAX function prediction analysis showed that a total of 14,822 ASVs (52,083 ASVs in total, and comment rate = 28 %) were annotated to 61 function groups. The present study considered the functions related to aerobic ammonia oxidation, nitrification, nitrate reduction and pathogens (animal parasites or symbionts, predatory or exoparasitic and human pathogens). In bulk soil, the relative abundance of the 4 functions was significantly affected by W treatments, but there was no significant difference among F treatments (Fig. 7A). Increased irrigation elevated the relative abundance of the 4 functions. In rhizosphere and endosphere, the relative abundance of the 4 functions was significantly affected by W and F treatments. Increased irrigation and addition of organic fertilizers enhanced the relative abundance of aerobic ammonia oxidation and nitrification, whereas reduced irrigation and addition of inorganic fertilizers decreased the relative abundance of the two functions. However, reducing irrigation and adding inorganic fertilizers increased the relative abundance of nitrate reduction and pathogens (Fig. 7, Table S6).

3.6. Effect of water and fertilization treatments on prokaryotic communities, plant nitrogen absorption and yield

The direct and indirect effects of W and F treatments on bulk soil, rhizosphere and endosphere prokaryotic microbial communities, PTN and wheat yield were analyzed by SEM. The model fitted well with the data (Fig. 8A, B, C), which explained 8.1 %, 82.1 % and 50.0 % of the variations of bulk soil, rhizosphere and endosphere prokaryotic microbial communities, 10 %–36.4 % of PTN variations and 33 % of wheat

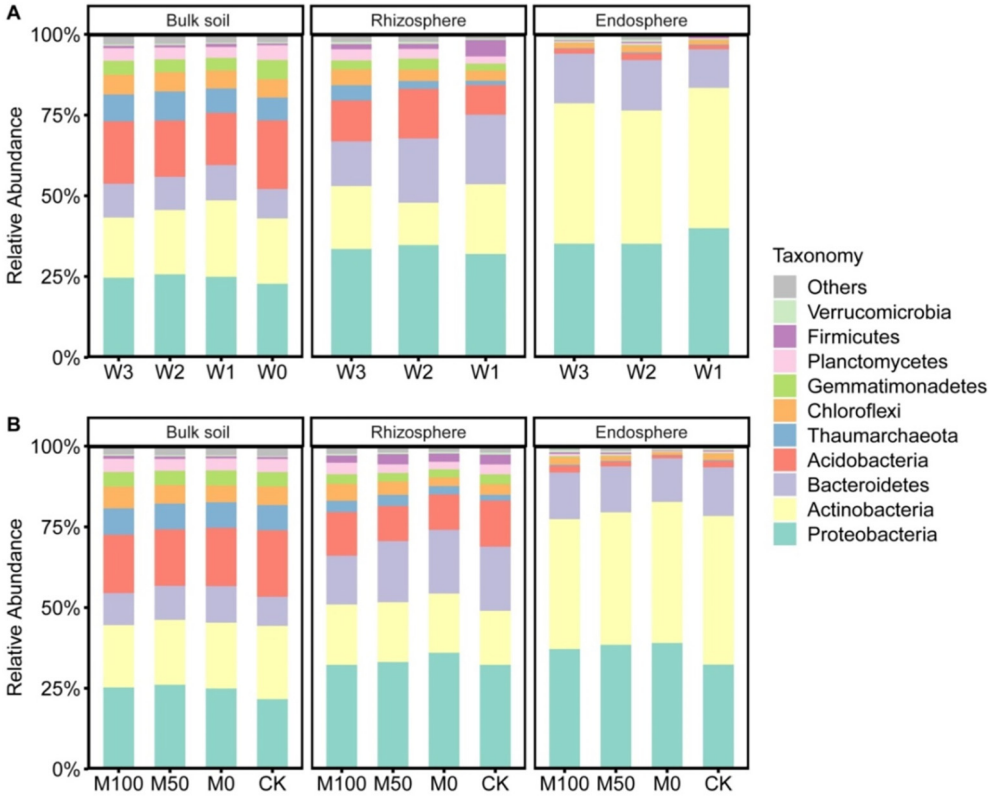


Fig. 4. Prokaryotic microbial community composition in bulk soil, rhizosphere and endosphere under different water and fertilization treatments at phylum level.

yield changes, respectively. Under the long-term water and fertilizer treatments, W treatments had more significant impact on wheat yield than F treatments. W treatments not only directly and significantly affected wheat yield ($P < 0.05$), but also improved nitrogen absorption (PTN) by regulating the prokaryotic microbial community in endosphere, which could significantly affect wheat yield ($P < 0.001$, Fig. 8C). The SEM was further constructed by SWC and SOM instead of W and F treatments, respectively. The model fitted well with the data (Fig. 8D, E, F), which explained 14.4 %, 55.8 % and 44.6 % of the variations of bulk soil, rhizosphere and endosphere prokaryotic microbial communities, 30.1 %–36.9 % of PTN variations and 29.4 % of wheat yield changes, respectively. Under the long-term water and fertilizer interaction treatment, SWC showed more significant impact on wheat yield than SOM. SWC directly and significantly influenced wheat yield ($P < 0.05$), and also improved nitrogen absorption (PTN) by regulating the prokaryotic microbial community in endosphere, hence significantly affected wheat yield ($P < 0.05$, Fig. 8F). Overall, irrigation and fertilization regimes regulated the prokaryotic microbial community and altered the SWC and SOM in the wheat root zone, thereby enhancing the nitrogen uptake and yield of wheat.

4. Discussion

The impact of long-term water and integrated fertilization on soil prokaryotic microbes and their association with wheat N uptake and yield still remains unknown. The results from the present study showed that long-term water and fertilizer treatments significantly altered prokaryotic microbial diversity and community structure in wheat root zone (bulk soil, rhizosphere and endosphere), and the W impact was more prominent. The water (W2) and fertilizer (M50 and M0) treatments improved the nitrogen absorption and wheat yield. The mechanisms of water and fertilizations on prokaryotic microorganisms in wheat root zone were discussed below.

4.1. Water levels more drastically affected the prokaryotic microbial community structure and diversity in bulk soil, rhizosphere and endosphere

Microorganisms in different niches of crop root zone are important to regulate host health and productivity (Bai et al., 2015; Qiu et al., 2019). Due to the different environments in the compartments of root zone, the physicochemical properties of different compartments may be varied (Fitzpatrick et al., 2020), which could lead to the selective supplement of microbial communities in the compartments (Fitzpatrick et al., 2018; Trivedi et al., 2020), resulting in changed microbial diversity and community composition in the compartments (Coleman-Derr et al., 2016).

The prokaryotic microorganisms in the root compartments responded differently to water and integrated fertilizations. In bulk soil, the alpha diversity was not affected by the fertilization regimes (Fig. 2), and this was in agreement with previous studies (Yang et al., 2018a; Liu et al., 2021). Many studies have shown that the alpha diversity of soil prokaryotic microorganisms was significantly affected by pH (Lauber et al., 2009; Yang et al., 2018b; Liu et al., 2021), and only when soil pH was significantly lowered (below 5) did it have a strong effect on prokaryotic microbial alpha diversity (Geisseler and Scow, 2014). In the current study, the soil pH varied from 8.15 to 8.39 under the fertilization treatments, which was not significantly affected by the treatments (Table S2), and thus the bulk soil prokaryotic alpha diversity was not considerably affected by the fertilization regimes (Fig. 2A, B). Nevertheless, in the rhizosphere and endosphere, increasing the amount of organic fertilizers, especially in the M100 treatment, significantly improved the alpha diversity of prokaryotic microorganisms. This may be ascribed to the low content of quick-acting nutrients such as nitrate in the organic fertilizers (Table S2). In order to obtain more nutrients, crops recruit prokaryotic microorganisms that decompose organic matter to accumulate in the rhizosphere (Micallef et al., 2014; Schlemper et al., 2017), thereby increasing the alpha diversity of rhizosphere prokaryotic microorganisms. These prokaryotic microorganisms may enter roots from the rhizosphere (Cordovez et al., 2019), thereby

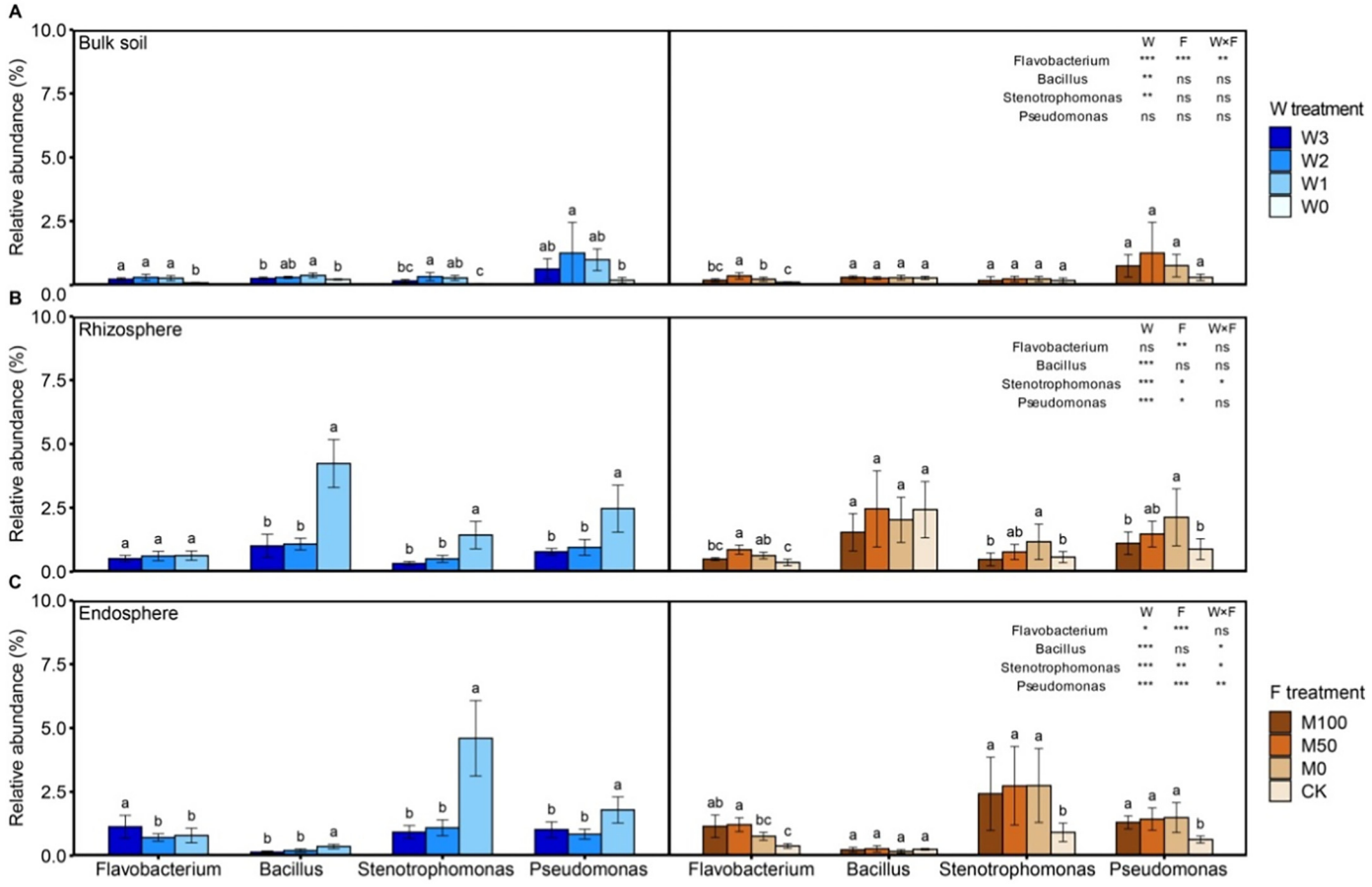


Fig. 5. The beneficial prokaryotic microorganisms in bulk soil, rhizosphere and endosphere under different water and fertilization treatments at genus level. W, F and W × F represent water treatment, fertilization treatment and their interaction, respectively. Different letters above the columns indicate significant differences among the treatments according to Duncan's multiple range test ($P < 0.05$). *, **, *** and ns indicate $P < 0.05$, $P < 0.01$, $P < 0.001$ and no significance, respectively.

increasing the alpha diversity of prokaryotic microorganisms in the endosphere. The biomarkers found through LEfSe analysis also demonstrated that the same biomarkers existed both in the rhizosphere and endosphere (Fig. S4).

Compared with W3 treatment, reducing irrigation increased the alpha diversity of bulk soil prokaryotic microorganisms. Excessive soil water content (such as in the W3 treatment) could reduce the heterogeneity of soil microsites, porosity and oxygen content, which was not conducive to the diversity of prokaryotic microorganisms and the coexistence of species (Frey, 2007). Consequently, reducing irrigation resulted in a decrease in the alpha diversity of rhizosphere prokaryotic microorganisms, which was in agreement with Liu et al. (2014b). The rhizosphere could provide a relatively stable living environment for prokaryotic microorganisms, and the root system can recruit prokaryotic microorganisms that are beneficial to crop growth by secreting small molecules to gather in the rhizosphere (Micallef et al., 2014; Schlemper et al., 2017), thereby increasing the alpha diversity of prokaryotic microorganisms in the rhizosphere. In consequence, the alpha diversity of endosphere prokaryotic microorganisms increased under elevated irrigation conditions due to the ability of rhizosphere prokaryotic microorganisms to enter the root (Fig. 2).

The prokaryotic microbial beta diversity displayed by PCoA showed that the effect of W treatments was greater than F treatments, particularly for rhizosphere prokaryotic microorganisms, which were clearly differentiated between different W treatments (Fig. 3C). The results of PEMANOVA analysis proved again that W treatments had a greater impact on the beta diversity of prokaryotic microbial than F treatments (Fig. 3), in line with the previous studies (Chen et al., 2020; Li et al., 2021). Similarly, the biomarkers under different W and F treatments from the LEfSe analysis showed that there were greater differences in prokaryotic microbial communities and more different prokaryotic (at genus level) under W treatments (Fig. S4), indicating further the more pronounced impact of W treatments on prokaryotic microbial community in different compartments than the F treatments.

The phylum level prokaryotic microbial composition in different compartments was significantly affected by W and F treatments (Fig. 4, Table S4). The predominant prokaryotic microbes at the phylum level in this study were similar to those in previous studies (Yang et al., 2018b; Cui et al., 2018; Bai et al., 2019). Increased irrigation improved the relative abundance of Proteobacteria and application of organic fertilizers increased the relative abundance of Firmicutes (Fig. 4, Table S4). Previous studies have shown that some prokaryotic microorganisms are beneficial for plant growth. For example, *Bacilli* is a beneficial bacterium that can promote plant growth and reduce the occurrence of plant diseases through a series of mechanisms (Aloo et al., 2019). *Flavobacterium* is usually isolated from plant rhizosphere and is associated with promoting plant growth (Schlaeppi et al., 2014). *Stenotrophomonas* and *Pseudomonas* are often endophytes that increase plant stress resistance (Jeong et al., 2021). Among the biomarkers identified by LEfSe analysis, the above four prokaryotic microorganisms are beneficial to plant growth (Fig. S4, Fig. 5). They showed different responses to water and fertilization treatments. Increasing irrigation improved the abundance of beneficial prokaryotic microorganisms in bulk soil, but decreased the abundance of them in rhizosphere and endosphere. This may be related to the fact that some beneficial bacteria such as *Stenotrophomonas* and *Pseudomonas* were generally enriched in crops in arid environments, which improved drought resistance by secreting biomass-promoting substances (Jeong et al., 2021). The application of organic fertilizers significantly increased the relative abundance of *Flavobacterium*, which was similar to the findings of Liu et al. (2021).

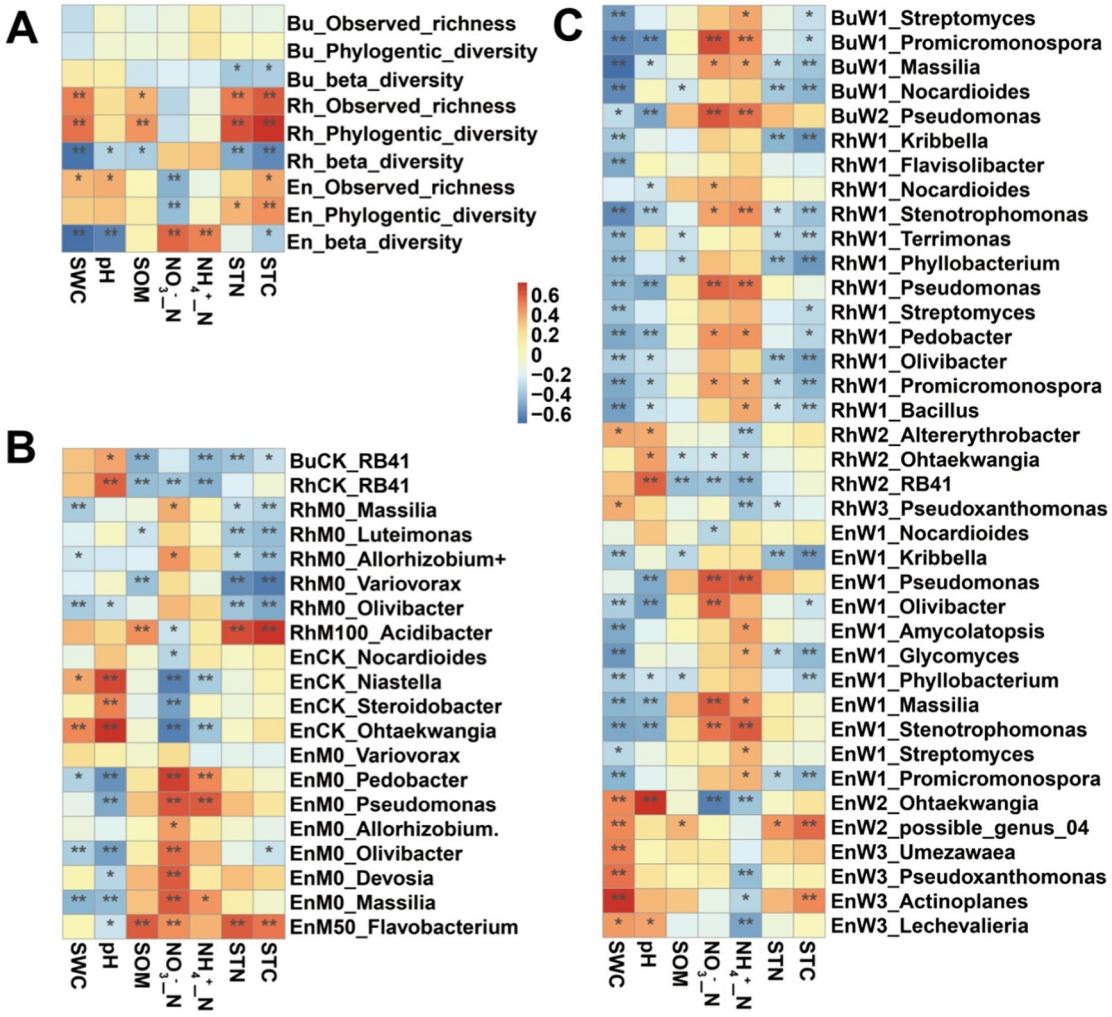


Fig. 6. Spearman correlation heat maps of environmental factors and alpha and beta diversity of prokaryotic communities in different compartments (A). Beta diversity is represented using the data on the first axis of PCoA. Spearman correlation heat maps of environmental factors and biomarkers of prokaryotic communities at genus level in different sample types (B and C). Red color indicates a positive correlation, and blue color denotes a negative correlation. Bu: bulk soil, Rh: rhizosphere, En: endosphere, *Allorhizobium* + : *Allorhizobium_Neorhizobium_Pararhizobium_Rhizobium*, SWC: soil water content, SOM: soil organic matter, NO_3^--N: soil nitrate nitrogen, NH_4^+-N: soil ammonium nitrogen, STN: soil total nitrogen, STC: soil total carbon (*$P < 0.05$; **$P < 0.01$).

4.2. SWC, NH_4^+-N and NO_3^--N were key predictors of prokaryotic microbial community composition under W and F treatments, respectively

Accumulated studies have shown that pH was an important factor affecting the structure of prokaryotic microbial communities (Fierer and Jackson, 2006; Rousk et al., 2010; Sun et al., 2015; Zhalnina et al., 2015; Zhou et al., 2015). The results in the present study also demonstrated the importance of pH in determining the prokaryotic microbial community structure in the wheat root zone. Soil pH was significantly correlated with most of the biomarkers under W and F treatments, whereas pH was significantly negatively associated with the beta diversity of rhizosphere and endosphere (Fig. 6). The alpha diversity of bulk soil had no significant correlation with the measured environmental factors, and this was in agreement with Liu et al. (2021). In addition, multiple studies have shown that SWC was also an important factor affecting the structure of prokaryotic microbial communities (McHugh and Schwartz, 2014; Bai et al., 2019). Nevertheless, the present study found that the biomarkers of different water treatments were found to have diverse correlations with SWC, namely, the biomarkers enriched in W1 treatment were negatively correlated with SWC, whereas those enriched in W2 and W3 treatments were positively related with SWC (Fig. 6C).

Changes in SWC and pH can increase the availability of various soil nutrients and promote the reproduction and growth of prokaryotic microorganisms (Chen et al., 2020; Li et al., 2021). In the current study, it was found that SWC was significantly negatively correlated with NH_4^+-N (Fig. S5), and the correlation between NH_4^+-N and the enriched biomarkers under water treatment was opposite to SWC. The present study also found that NO_3^--N had different relations with biomarkers under different fertilization treatments, and the biomarkers enriched in inorganic fertilizer treatments (M0 and M50) were positively associated with NO_3^--N, whereas biomarkers enriched in CK and M100 treatments were negatively correlated with NO_3^--N (Fig. 6B). Therefore, SWC and NH_4^+-N were key predictors of prokaryotic microbial community composition under W treatments, while soil NO_3^--N was a key predictor of prokaryotic microbial community composition under F treatments. In addition, previous studies have reported that STC and STN were important environmental factors affecting the changes of prokaryotic microbial communities (Wang et al., 2018b; Zhang et al., 2019), and in good agreement with this, it was found that STC, STN and prokaryotic microbial diversity and most biomarkers were significantly correlated (Fig. 6).

4.3. Increased irrigation and application of organic fertilizers were beneficial to increase aerobic ammonium oxidation and nitrification-related functional prokaryotic microorganisms in the rhizosphere and endosphere

In bulk soil, the FAPROTAX function prediction showed that the four focused functions (aerobic ammonia oxidation, nitrification, nitrate reduction

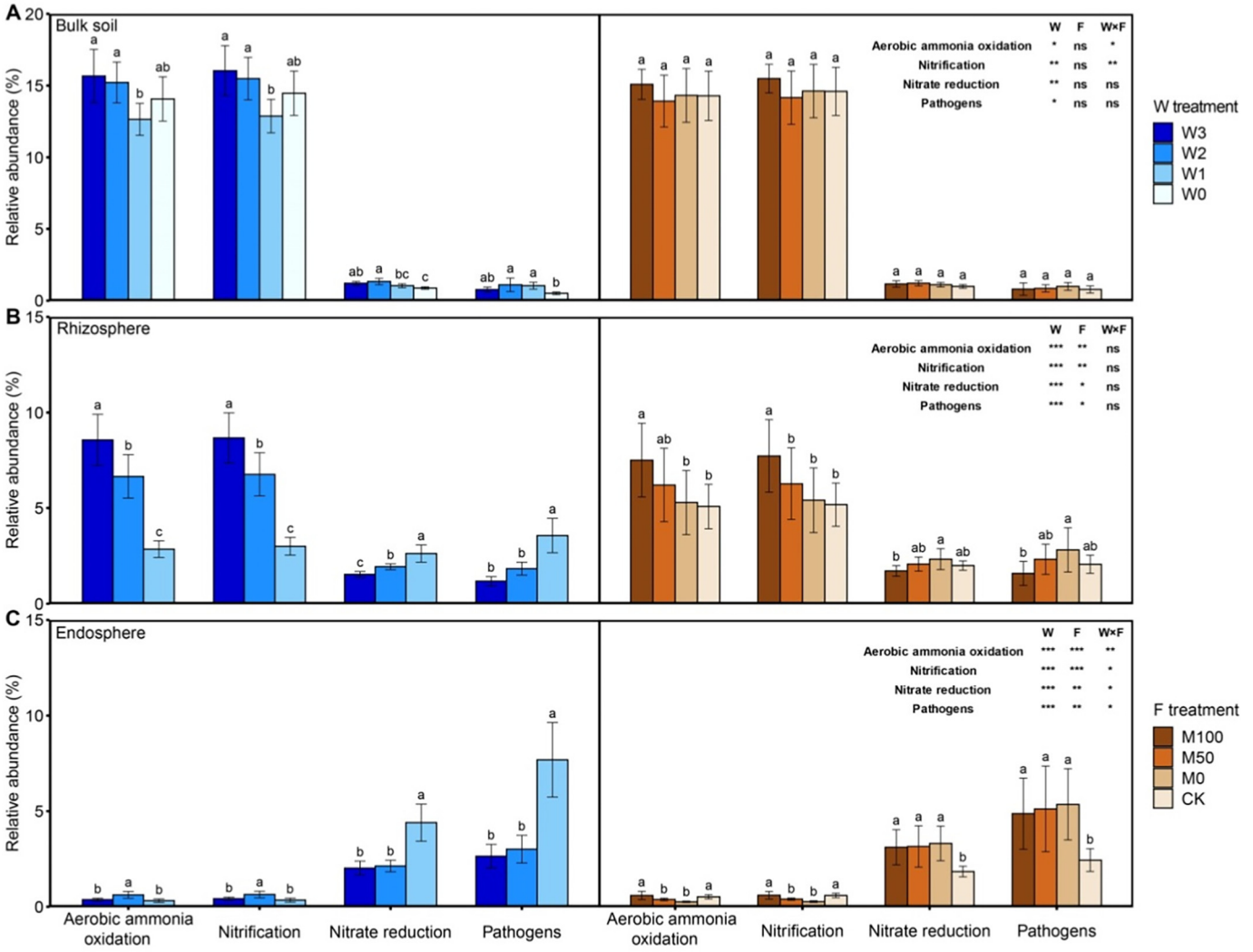


Fig. 7. Functions of the prokaryotic microbial communities predicted by FAPROTAX. W, F and W × F represent water treatment, fertilization treatment and their interaction, respectively. Different letters above the columns indicate significant differences among the treatments according to Duncan's multiple range test ($P < 0.05$). *, **, *** and ns indicate $P < 0.05$, $P < 0.01$, $P < 0.001$ and no significance, respectively.

and pathogens) were similar among the F treatments (Fig. 7A), and this was consistent with the observed results of alpha diversity in bulk soil (Fig. 2). However, increasing irrigation elevated the relative abundance of the four functions in bulk soil, probably due to the improved SWC and nutrient dissolution in the soil (McHugh and Schwartz, 2014; Zhou et al., 2015), making nitrogen metabolism-related prokaryotes microbial communities increase. Due to the competitive relationship between microorganisms (Fredrickson and Stephanopoulos, 1981), the increase of nitrogen metabolism-related prokaryotic microbial communities may affect the survival of other species of prokaryotic microorganisms, thereby affecting community diversity. In rhizosphere and endosphere, increased irrigation and added organic fertilizers increased the relative abundance of aerobic ammonia oxidation and nitrification (Fig. 7B, C). This could owe to the increased relative abundance of aerobic ammonia oxidation and nitrification in bulk soil (Fig. 7A), or by the leaching of nitrate caused by increased irrigation, resulting in a reduction in the reaction products of some microorganisms (such as *Nitrospira* that could oxidize ammonia to nitrous acid, which was key to control the rate of nitrification), and the increase of functional microorganisms related to aerobic ammonia oxidation and nitrification through feedback to ensure the uptake of nitrogen by wheat roots (Li et al., 2021). The application of organic fertilizers led to an increase in the relative abundances of aerobic ammonia oxidation and nitrification, probably ascribing to the lack of available nutrients in organic fertilization treatments. In order to ensure the absorption of nitrogen in wheat roots, functional microorganisms related to aerobic ammonia oxidation and nitrification were recruited (Micallef et al., 2014; Schlemper et al., 2017; Ouyang et al., 2018). In addition, reducing irrigation and adding inorganic fertilizers increased the relative abundance of nitrate reduction and pathogens in rhizosphere and endosphere, which was not conducive to crop health and nutrient absorption and utilization. This was possibly caused by the competitive relationship between microorganisms (Fredrickson and Stephanopoulos, 1981), and the reduction of irrigation reduced the functional microorganisms related to aerobic ammonia oxidation and nitrification, whereas the functional microorganisms related to nitrate reduction and pathogens increased. Previous studies have shown that rhizosphere is a playground for pathogenic microorganisms (Raaijmakers et al., 2009), and the addition of organic fertilizers can stimulate the activity of beneficial microorganisms, thereby inhibiting pathogenic microorganisms (Hoitink and Boehm, 1999), which may be the reason why the relative abundance of pathogens under M0 treatment was higher than that under M100 treatment. The increase of microorganisms related to nitrate reduction in M0 treatment may be caused by the increase of denitrification reaction substrates in the rhizosphere. Therefore, increasing irrigation and applying organic fertilizers increased nitrogen uptake in wheat and reduced the occurrence of diseases.

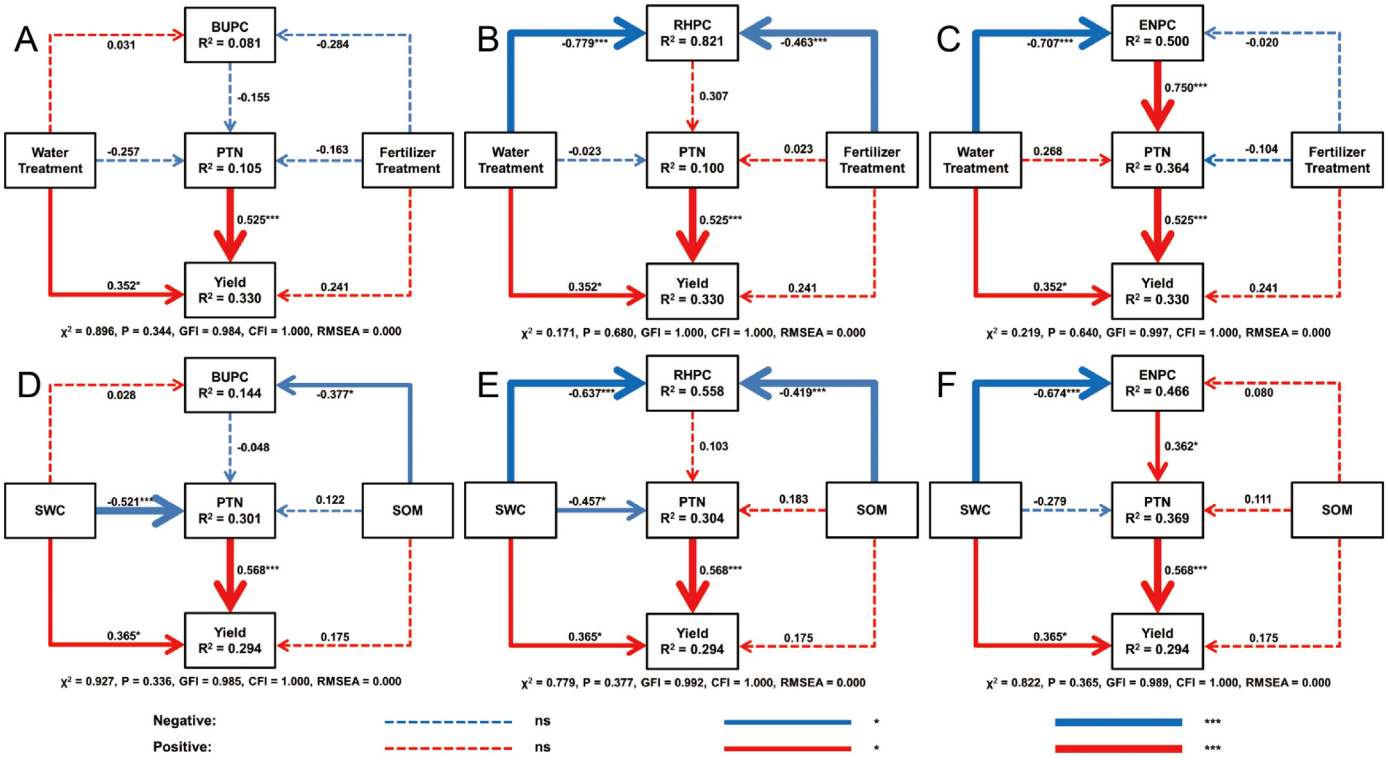


Fig. 8. SEM of bulk soil (A), rhizosphere (B), endosphere prokaryotic microbial communities (C), plant total nitrogen (PTN) and yield under water and fertilizer treatments. SEM of bulk soil (D), rhizosphere (E), endosphere prokaryotic microbial communities (F), plant total nitrogen (PTN) and yield under soil water content (SWC) and soil organic matter (SOM). The red line represents the positive path coefficient and the blue line denotes the negative path coefficient (*$P < 0.05$; ***$P < 0.001$). BUPC: bulk soil prokaryotic microbial communities, RHPC: rhizosphere prokaryotic microbial communities, ENPC: endosphere prokaryotic microbial communities.

4.4. Water and fertilizer regimes promoted nitrogen uptake and wheat yield by regulating prokaryotic microorganisms in wheat root zone

Crop growth and yield are determined by water and nutrient supply (Wang et al., 2018a). Application of organic fertilizers increased the content of soil organic matter (Table S2), contributing to increasing crop yields (Wang et al., 2015; Liu et al., 2021). In the current study, STN was significantly positively correlated with SOM, which was also significantly associated with wheat yield (Fig. S5), indicating the importance of increasing soil organic matter to improve crop yield production, though there was no significant difference in wheat yield between organic fertilizer and inorganic fertilizer treatment (Fig. 1). Irrigation and fertilization also changed other soil physicochemical properties. Irrigation increased SWC and soil pH (Table S2), and there was a significant positive correlation between soil pH and SWC (Fig. S5). This may be due to the fact that irrigation reduced the oxygen content of the bulk soil, and promoted the denitrification process (Zhang et al., 2014). Nonetheless, the application of inorganic fertilizers significantly reduced soil pH, which was related to the formation of hydrogen ions by nitrification in the soil (Zhou et al., 2014; Carrara et al., 2018; Yang et al., 2018b). It is reported that the growth and yield of crops are affected by soil pH (Baquy et al., 2018; Pan et al., 2020), and the current study showed that soil pH was significantly negatively associated with wheat yield (Fig. S5).

Soil nutrients changed significantly under different W and F treatments, especially in the organic fertilizer treatments (M100 and M50), where STN and STC increased significantly. However, compared with CK treatment, inorganic fertilizer treatment did not affect STN and STC (Table S2), indicating that long-term organic fertilizer improved soil fertility level (Blair et al., 2006; Liang et al., 2012; Ozlu and Kumar, 2018). Previous studies have shown that increasing the content of available nutrients such as available nitrogen in soil improved crop yield (Gondwe et al., 2020). In the current study, soil available nitrogen (ammonium nitrogen and nitrate nitrogen) was significantly positively associated with nitrogen uptake, affecting wheat yield (Fig. 1). Thus, the changed soil SOM, pH, NH_4^+-N and NO_3^--N had altered the nutrient uptake and wheat yield.

In the current study, SWC and SOM increased with the elevated irrigation and organic fertilizer application (Table S2). They are important factors affecting microorganisms (Wu et al., 2011; Liu et al., 2014a, 2014b; Zhou et al., 2015). In the present study, the changes in SWC and SOM led to changes in the diversity and community structure of prokaryotic microorganisms (Figs. 2, 3, 4). Liu et al. (2021) reported that the application of organic fertilizer affected the soil microbial communities and then the soil enzyme activity, leading to changes in soil nutrients, thereby affecting crop yields. Sun et al. (2021) found that different fertilization treatments influenced the microbial diversity by changing soil characteristics, thereby affecting the yields. By constructing SEM, it was found that W and F treatments affected the nitrogen uptake and yield of wheat by regulating the prokaryotic microbial community in different compartments of the wheat root zone. This was further demonstrated from constructing SEM by SWC and SOM instead of W and F treatments, respectively. Therefore, water and fertilizer treatments regulated the prokaryotic microbial communities of bulk soil, rhizosphere and endosphere by changing the soil water content (SWC) and soil organic matter (SOM), which consequently led to the variations in nitrogen uptake and yield of wheat.

5. Conclusions

The long-term different irrigation and fertilization regimes changed the physical and chemical properties of the soil, thereby affecting the community structure of prokaryotic microbes. Water treatment had a more significant impact on the diversity and composition of prokaryotic microbial communities in different compartments, and application of organic fertilizers increased the diversity of prokaryotic microorganisms and the relative abundance of functional microorganisms related to aerobic ammonia

oxidation and nitrification in the rhizosphere and endosphere. SWC and NH_4^+-N as well as NO_3^--N were key predictors of prokaryotic microbial community composition under W and F treatments, respectively. Long-term irrigation and fertilization changed the prokaryotic microbial communities in different compartments by altering SWC and SOM, thereby affecting nitrogen uptake and significantly promoting wheat yield. Collectively, appropriate addition of organic fertilizers (M50, 50 % organic fertilizers and 50 % inorganic fertilizers) under W2 (pre-sowing irrigation and jointing irrigation) irrigation conditions reduced the amount of chemical fertilizer and irrigation water application, while improved soil organic matter and nutrient content, and increased prokaryotic microorganisms diversity to achieve less resource input while enhanced nutrient absorption and wheat yield.

CRediT authorship contribution statement

Conception and design: Wenying Zhang, Minjie Yao, Yaosheng Wang; Formal analysis and investigation: Chao Wang, Haiyang Ma, Zhihan Feng, Zhenxing Yan, Bolong Song, Jialong Wang, Yuyin Zheng; Draft conceptualization: Chao Wang, Minjie Yao; Writing - original draft preparation: Chao Wang; Writing - review and editing: Chao Wang, Haiyang Ma, Yaosheng Wang, Wenying Zhang, Minjie Yao, Weiping Hao; All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the National Key Research and Development Program of China (2018YFE0107000), China Agricultural Research System (CARS-06-14.5-A34), HAAFS Science and Technology Innovation Special Project (2022KJCXZX-HZS-3).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.156952.

References

Aloo, B.N., Makumba, B.A., Mbega, E.R., 2019. The potential of Bacilli rhizobacteria for sustainable crop production and environmental sustainability. Microbiol. Res. 219, 26–39. https://doi.org/10.1016/j.micres.2018.10.011.

Bai, Y., Muller, D.B., Srinivas, G., Garrido-Oter, R., Potthoff, E., Rott, M., Dombrowski, N., Munch, P.C., Spaepen, S., Remus-Emsermann, M., Huttel, B., McHardy, A.C., Vorholt, J.A., Schulze-Lefert, P., 2015. Functional overlap of the Arabiodopsis leaf and root microbiota. Nature 528, 364–369. https://doi.org/10.1038/nature16192.

Bai, H., He, S., Qin, T., Yan, D., Weng, B., Zhao, X., Li, X., Bai, Y., Ma, J., 2019. Influences of irrigation amount on the rhizospheric microorganism composition and carbon dioxide flux of maize crops. Geoderma 343, 1–9. https://doi.org/10.1016/j.geoderma.2019.02.022.

Baquy, M.A.A., Li, J., Jiang, J., Mehmood, K., Shi, R., Xu, R., 2018. Critical pH and exchangeable Al of four acidic soils derived from different parent materials for maize crops. J. Soil Sediments 18, 1490–1499. https://doi.org/10.1007/s11368-017-1887-x.

Bastida, F., Torres, I.F., Hernández, T., García, C., 2017. The impacts of organic amendments: do they confer stability against drought on the soil microbial community? Soil Biol. Biochem. 113, 173–183. https://doi.org/10.1016/j.soilbio.2017.06.012.

Bei, S., Zhang, Y., Li, T., Christie, P., Li, X., Zhang, J., 2018. Response of the soil microbial community to different fertilizer inputs in a wheat-maize rotation on a calcareous soil. Agric. Ecosyst. Environ. 260, 58–69. https://doi.org/10.1016/j.agee.2018.03.014.

Blair, N., Faulkner, R.D., Till, A.R., Korschens, M., Schulz, E., 2006. Long-term management impacts on soil C, N and physical fertility: part II: bad Lauchstadt static and extreme FYM experiments. Soil Tillage Res. 91, 39–47. https://doi.org/10.1016/j.still.2005.11.001.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: high-resolution sample inference fromIllumina amplicon data. Nat. Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869.

Carrara, J.E., Walter, C.A., Hawkins, J.S., Peterjohn, W.T., Averill, C., Brzostek, E.R., 2018. Interactions among plants, bacteria, and fungi reduce extracellular enzyme activities under long-term N fertilization. Glob. Chang. Biol. 24, 2721–2734. https://doi.org/10.1111/gcb. 14081.

Chen, Z., Wang, H., Liu, X., Zhao, X., Li, C., 2017. Changes in soil microbial community and organic carbon fractions under short-term straw return in a rice–wheat cropping system. Soil Tillage Res. 165, 121–127. https://doi.org/10.1016/j.still.2016.07.018.

Chen, J., Luo, Y.Q., van Groenigen, K.J., Hungate, B.A., Cao, J.J., Zhou, X.H., Wang, R.W., 2018. A keystone microbial enzyme for nitrogen control of soil carbon storage. Sci. Adv. 4, 1–6. https://doi.org/10.1126/sciadv.aaq1689.

Chen, L., Li, C., Feng, Q., Wei, Y., Zhao, Y., Zhu, M., Deo, R., 2020. An integrative influence of saline water irrigation and fertilization on the structure of soil bacterial communities. J. Agric. Sci. 157, 1–8. https://doi.org/10.1126/sciadv.aaq1689.

Coleman-Derr, D., Desgarennes, D., Fonseca-Garcia, C., Gross, S., Clingenpeel, S., Woyke, T., North, G., Visel, A., Partida-Martinez, L.P., Tringe, S.G., 2016. Plant compartment and biogeography affect microbiome composition in cultivated and native agave species. New Phytol. 209 (2), 798–811. https://doi.org/10.1111/nph.13697.

Corato, U.D., 2020. Agricultural waste recycling in horticultural intensive farming systems by on-farm composting and compost-based tea application improves soil quality and plant health: a review under the perspective of a circular economy. Sci. Total Environ. 738, 139840. https://doi.org/10.1016/J.SCITOTENV.2020.139840.

Cordovez, V., Dini-Andreote, F., Carrión, V.J., Raaijmakers, J.M., 2019. Ecology and evolution of plant microbiomes. Annu. Rev. Microbiol. 73 (1), 1–20. https://doi.org/10.1146/annurev-micro-090817-062524.

Cui, X.W., Zhang, Y.Z., Gao, J.S., Peng, F.Y., Gao, P., 2018. Long-term combined application of manure and chemical fertilizer sustained higher nutrient status and rhizospheric bacterial diversity in reddish paddy soil of central South China. Sci. Rep. 8, 1–11. https://doi.org/10.1038/s41598-018-34685-0.

Davide, F., Elke, S., Guillaume, L., Tesfaye, W., Francois, B., Thomas, R., 2016. Mineral vs. organic amendments: microbial community structure, activity and abundance of agriculturally relevant microbes are driven by long-term fertilization strategies. Front. Microbiol. 7, 289. https://doi.org/10.3389/fmicb.2016.01446.

Dikgwatlhe, S.B., Chen, Z.D., Lal, R., Zhang, H.L., Chen, F., 2014. Changes in soil organic carbon and nitrogen as affected by tillage and residue management under wheat-maize cropping system in the North China Plain. Soil Tillage Res. 144, 110–118. https://doi.org/10.1016/j.still.2014.07.014.

Ding, J., Jiang, X., Ma, M., Zhou, B., Guan, D., Zhao, B., Zhou, J., Cao, F., Li, L., Li, J., 2016. Effect of 35 years inorganic fertilizer and manure amendment on structure of bacterial and archaeal communities in black soil of northeast China. Appl. Soil Ecol. 105, 187–195. https://doi.org/10.1016/j.apsoil.2016.04.010.

Edwards, J.A., Santos-Medellin, C.M., Liechty, Z.S., Nguyen, B., Lurie, E., 2018. Compositional shifts in root-associated bacterial and archaeal microbiota track the plant life cycle in field-grown rice. PLoS Biol. 16, 1–28. https://doi.org/10.1371/journal.pbio.2003862.

Feng, Y., Chen, R., Hu, J., Zhao, F., Wang, J., Chu, H., Zhang, J., Dolfing, J., Lin, X., 2015. *Bacillus asahii* comes to the fore in organic manure fertilized alkaline soils. Soil Biol. Biochem. 81, 186–194. https://doi.org/10.1016/j.soilbio.2014.11.021.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proc. Natl. Acad. Sci. U. S. A. 103, 626–631. https://doi.org/10.1073/pnas.0507535103.

Fitzpatrick, C.R., Copeland, J., Wang, P.W., Guttman, D.S., Kotanen, P.M., Johnson, M.T.J., 2018. Assembly and ecological function of the root microbiome across angiosperm plant species. Proc. Natl. Acad. Sci. U. S. A. 115, E1157–E1165. https://doi.org/10.1073/pnas.1717617115.

Fitzpatrick, C.R., Salas-Gonzalez, I., Conway, J.M., Finkel, O.M., Gilbert, S., Russ, D., Teixerira, P.J.P.L., Dangl, J.L., 2020. The plant microbiome: from ecology to reductionism and beyond. Annu.Rev.Microbiol. 74, 81–100. https://doi.org/10.1146/annurev-micro-022620- 014327.

Fredrickson, A., Stephanopoulos, G., 1981. Microbial competition. Science 213 (4511), 972–979. https://doi.org/10.1126/science.7268409.

Frenk, S., Hadar, Y., Minz, D., 2014. Resilience of soil bacterial community to irrigation with water of different qualities under mediterranean climate. Environ. Microbiol. 16, 559–569. https://doi.org/10.1111/1462-2920.12183.

Frey, S.D., 2007. Spatial distribution of soil organisms. In: Paul, E.A. (Ed.), Soil Microbiology, Ecology and Biochemistry, 3rd edn. Academic Press, San Diego, CA, pp. 283–300 https://doi.org/10.1016/B978-0-08-047514-1.50015-9.

Geisseler, D., Scow, K.M., 2014. Long-term effects of mineral fertilizers on soil microorganisms – a review. Soil Biol. Biochem. 75, 54–63. https://doi.org/10.1016/j.soilbio.2014.03.023.

Gondwe, R.L., Kinoshita, R., Suminoe, T., Aiuchi, D., Palta, J.P., Tani, M., 2020. Available soil nutrients and NPK application impacts on yield, quality, and nutrient composition of potatoes growing during the main season in Japan. Am. J. Potato Res. 97, 234–245. https://doi.org/10.1007/s12230-020-09776-2.

Guo, J.H., Liu, X.J., Zhang, Y., Shen, J.L., Han, W.X., Zhang, W.F., Christie, P., Goulding, K.W., Vitousek, P.M., Zhang, F.S., 2010. Significant acidification in major Chinese croplands. Science 327, 1008–1010. https://doi.org/10.1126/science.1182570.

Guo, J., Liu, W., Zhu, C., Luo, G., Kong, Y., Ling, N., Wang, M., Dai, J., Shen, Q., Guo, S., 2018. Bacterial rather than fungal community composition is associated with microbial activities and nutrient-use efficiencies in a paddy soil with short-term organic amendments. Plant Soil 424 (1–2), 335–349. https://doi.org/10.1007/s11104-017-3547-8.

Hartmann, M., Frey, B., Mayer, J., Mder, P., Widmer, F., 2015. Distinct soil microbial diversity under long-term organic and conventional farming. ISME J. 9 (5), 1177–1194. https://doi.org/10.1038/ismej.2014.210.

Henry, H., 2012. Soil extracellular enzyme dynamics in a changing climate. Soil Biol. Biochem. 47, 53–59. https://doi.org/10.1016/j.soilbio.2011.12.026.

Hoitink, H., Boehm, M., 1999. Biocontrol within the context of soil microbial communities: a substrate-dependent phenomenon. Annu. Rev. Phytopathol. 37, 427–446. https://doi.org/10.1146/annurev.phyto.37.1.427.

Hu, X., Liu, J., Wei, D., Zhu, P., Cui, X., Zhou, B., Chen, X., Jin, J., Liu, X., Wang, G., 2018. Soil bacterial communities under different long-term fertilization regimes in three locations

across the black soil region of northeast China. Pedosphere 28 (5), 751–763. https://doi.org/10.1016/S1002- 0160(18)60040-2.
Igalavithana, A.D., Lee, S.S., Niazi, N.K., Lee, Y.H., Kim, K.H., Park, J.H., Moon, D.H., Ok, Y.S., 2017. Assessment of soil health in urban agriculture: soil enzymes and microbial properties. Sustainability 9, 1–14. https://doi.org/10.3390/su9020310.
Ikoyi, I., Egeter, B., Chaves, C., Ahmed, M., Fowler, A., Schmalenberger, A., 2020. Responses of soil microbiota and nematodes to application of organic and inorganic fertilizers in grassland columns. Biol. Fertil. Soils 56, 647–662. https://doi.org/10.1007/s00374-020-01440-5.
Jannoura, R., Joergensen, R., Bruns, C., 2014. Organic fertilizer effects on growth, crop yield, and soil microbial biomass indices in sole and intercropped peas and oats under organic farming conditions. Eur. J. Agron. 52, 259–270. https://doi.org/10.1016/j.eja.2013.09. 001.
Jeong, S., Kim, T.M., Choi, B., Kim, Y., Kim, E., 2021. Invasive Lactuca serriola seeds contain endophytic bacteria that contribute to drought tolerance. Sci. Rep. 11 (1), 13307. https://doi.org/10.1038/s41598-021-92706-x.
Ji, L., Wu, Z., You, Z., Yi, X., Ni, K., Guo, S., Ruan, J., 2018. Effects of organic substitution for synthetic n fertilizer on soil bacterial diversity and community composition: a 10-year field trial in a tea plantation. Agric. Ecosyst. Environ. 268, 124–132. https://doi.org/10.1016/j.agee.2018.09.008.
Kumar, U., Nayak, A.K., Shahid, M., Gupta, V., Panneerselvam, P., Mohanty, S., Kaviraj, M., Kumar, A., Chatterjee, D., Lal, B., 2018. Continuous application of inorganic and organic fertilizers over 47 years in paddy soil alters the bacterial community structure and its influence on rice production. Agric. Ecosyst. Environ. 262, 65–75. https://doi.org/10.1016/j.agee.2018.04.016.
Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Appl. Environ. Microbiol. 75 (15), 5111–5120. https://doi.org/10.1128/aem.00335-09.
Li, F., Chen, L., Zhang, J., Yin, J., Huang, S., 2017. Bacterial community structure after long-term organic and inorganic fertilization reveals important associations between soil nutrients and specific taxa involved in nutrient transformations. Front. Microbiol. 8, 187. https://doi.org/10.3389/fmicb.2017.00187.
Li, H., Wang, H., Jia, B., Li, D., Li, R., 2021. Irrigation has a higher impact on soil bacterial abundance, diversity and composition than nitrogen fertilization. Sci. Rep. 11 (1). https://doi.org/10.1038/s41598-021-96234-6.
Liang, Q., Chen, H.Q., Gong, Y.S., Fan, M.S., Yang, H.F., Lal, R., Kuzyakov, Y., 2012. Effects of 15 years of manure and inorganic fertilizers on soil organic carbon fractions in a wheat-maize system in the North China plain. Nutr. Cycl. Agroecosyst. 92, 21–33. https://doi.org/10.1007/s10705-011-9469-6.
Ling, N., Sun, Y.M., Ma, J.H., Guo, J.J., Zhu, P., Peng, C., Yu, G.H., Ran, W., Guo, S.W., Shen, Q.R., 2014. Response of the bacterial diversity and soil enzyme activity in particle-size fractions of mollisol after different fertilization in a long-term experiment. Biol. Fertil. Soils 50, 901–911. https://doi.org/10.1007/s00374-014-0911-1.
Liu, H., Brettell, L.E., 2019. Plant defense by VOC-induced microbial priming. Trends Plant Sci. 24, 187–189. https://doi.org/10.1016/j.tplants.2019.01.008.
Liu, H., Carvalhais, L.C., Crawford, M., Singhm, E., Dennis, P.G., Pieterse, C.M.J., Schenk, P.M., 2017. Inner plant values: diversity, colonization and benefits from endophytic bacteria. Front. Microbiol. 8, 1–17. https://doi.org/10.3389/fmicb.2017.02552.
Liu, J., Shu, A., Song, W., Shi, W., Li, M., Zhang, W., Li, Z., Liu, G., Yuan, F., Zhang, S., Liu, Z., Gao, Z., 2021. Long-term organic fertilizer substitution increases rice yield by improving soil properties and regulating soil bacteria. Geoderma 404, 115287. https://doi.org/10.1016/j.geoderma. 2021.115287.
Liu, J., Sui, Y., Yu, Z., Shi, Y., Chu, H., Jin, J., Liu, X., Wang, G., 2014a. High throughput sequencing analysis of biogeographical distribution of bacterial communities in the black soils of Northeast China. Soil Biol. Biochem. 70, 113–122. https://doi.org/10.1016/j.soilbio.2013.12.014.
Liu, F., Xing, S., Ma, H., Chen, B., Du, B., 2014b. Effects of continuous drought on soil bacteria populations and community diversity in sweet cherry rhizosphere. Acta Ecol. Sin. 34 (3), 642–649. https://doi.org/10.5846/stxb201211061552.
McHugh, T.A., Schwartz, E., 2014. Changes in plant community composition and reduced precipitation have limited effects on the structure of soil bacterial and fungal communities present in a semiarid grassland. Plant Soil 388, 175–186. https://doi.org/10.1007/s11104-014-2269-4.
Micallef, S.A., Channer, S., Shiaris, M.P., Colón-Carmona, A., 2014. Plant age and genotype impact the progression of bacterial community succession in the Arabidopsis rhizosphere. Plant Signal.Behav. 4, 777–780. https://doi.org/10.4161/psb.4.8.9229.
Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biol. Biochem. 59, 72–85. https://doi.org/10.1016/j.soilbio.2013.01.002.
Orr, C.H., Carlo, L., Cummings, S.P., Cooper, J.M., Mark, I.A., 2012. Impacts of organic and conventional crop management on diversity and activity of free-living nitrogen fixing bacteria and total bacteria are subsidiary to temporal effects. PLoS One 7 (12), e52891. https://doi.org/10.1371/journal.pone.0052891.
Ouyang, Y., Reeve, J.R., Norton, J.M., 2018. Soil enzyme activities and abundance of microbial functional genes involved in nitrogen transformations in an organic farming system. Biol. Fertil. Soils 54, 437–450. https://doi.org/10.1007/s00374-018-1272-y.
Ozlu, E., Kumar, S., 2018. Response of soil organic carbon, pH, electrical conductivity, and water stable aggregates to long-term annual manure and inorganic fertilizer. Soil Sci. Soc. Am. J. 82, 1243–1251. https://doi.org/10.2136/sssaj2018.02.0082.
Pan, X., Baquy, A.A., Guan, P., Yan, J., Xie, L., 2020. Effect of soil acidification on the growth and nitrogen use efficiency of maize in ultisols. J. Soils Sediments 20 (7). https://doi.org/10.1007/s11368-019-02515-z.
Preece, C., Verbruggen, E., Liu, L., Weedon, J.T., Peñuelas, J., 2019. Effects of past and current drought on the composition and diversity of soil microbial communities. Soil Biol. Biochem. 131, 28–39. https://doi.org/10.1016/j.soilbio.2018.12.022.
Qaswar, M., Jing, H., Ahmed, W., Li, D.C., Liu, S.J., Lu, Z., Cai, A.D., Liu, L.S., Xu, Y.M., Gao, J.S., Zhang, H.M., 2020. Yield sustainability, soil organic carbon sequestration and nutrients balance under long-term combined application of manure and inorganic fertilizers in acidic paddy soil. Soil Tillage Res. 198, 1–6. https://doi.org/10.1016/j.still.2019.104569.
Qiu, Z., Egidi, E., Liu, H., Kaur, S., Singh, B.K., 2019. New frontiers in agriculture productivity: optimised microbial inoculants and in situ microbiome engineering. Biotechnol. Adv. 37, 107371. https://doi.org/10.1016/j.biotechadv.2019.03.010.
Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., Glockner, F.O.F., 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41, D590–D596. https://doi.org/10.1093/nar/gks1219.
Quemada, M., Gabriel, J.L., 2016. Approaches for increasing nitrogen and water use efficiency simultaneously. Glob.Food Secur. 9, 29–35. https://doi.org/10.1016/j.gfs.2016.05.004.
Raaijmakers, J.M., Paulitz, T.C., Steinberg, C., Alabouvette, C., Moënne-Loccoz, Y., 2009. The rhizosphere: a playground and battlefield for soilborne pathogens and beneficial microorganisms. Plant Soil 321 (1), 341–361. https://doi.org/10.1007/s11104-008-9568-6.
Ramirez, K.S., Lauber, C.L., Knight, R., Bradford, M.A., Fierer, N., 2010. Consistent effects of nitrogen fertilization on soil bacterial communities in contrasting systems. Ecology 91, 3463–3470. https://doi.org/10.1890/10-0426.1.
Rousk, J., Bååth, E., Brookes, P.C., Lauber, C.L., Lozupone, C., Caporaso, J.G., Knight, R., Fierer, N., 2010. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J. 4, 1340–1351. https://doi.org/10.1038/ismej.2010.58.
Schlaeppi, K., Dombrowski, N., Oter, R.G., van Themaat, E.V.L., Schulze-Lefert, P., 2014. Quantitative divergence of the bacterial root microbiota in Arabidopsis thaliana relatives. Proc. Natl. Acad. Sci. U. S. A. 111, 585–592. https://doi.org/10.1073/pnas.1321597111.
Schlemper, T.R., Leite, M., Lucheta, A.R., Shimels, M., Kuramae, E.E., 2017. Rhizobacterial community structure differences among sorghum cultivars in different growth stages and soils. FEMS Microbiol. Ecol. 93 (8), 1–11. https://doi.org/10.1093/femsec/fix096.
Sebilo, M., Mayer, B., Nicolardot, B., Pinay, G., 2013. Long-term fate of nitrate fertilizer in agricultural soils. Proc. Natl. Acad. Sci. U. S. A. 110 (45), 18185–18189. https://doi.org/10.1073/pnas.1305372110.
Sessitsch, A., Mitter, B., 2015. 21st century agriculture: integration of plant microbiomes for improved crop production and food security. Microb. Biotechnol. 8, 32–33. https://doi.org/10.1111/1751-7915.12180.
Shen, J.P., Zhang, L.M., Guo, J.F., Ray, J.L., He, J.Z., 2010. Impact of long-term fertilization practices on the abundance and composition of soil bacterial communities in Northeast China. Appl. Soil Ecol. 46, 119–124. https://doi.org/10.1016/j.apsoil.2010.06.015.
Sun, R., Zhang, X.X., Guo, X., Wang, D., Chu, H., 2015. Bacterial diversity in soils subjected to long-term chemical fertilization can be more stably maintained with the addition of livestock manure than wheat straw. Soil Biol. Biochem. 88, 9–18. https://doi.org/10.1016/j.soilbio.2015.05.007.
Sun, A., Jiao, X., Chen, Q., Wu, A., Zheng, Y., Lin, Y., He, J., Hu, H., 2021. Microbial communities in crop phyllosphere and root endosphere are more resistant than soil microbiota to fertilization. Soil Biol. Biochem. 153, 108113. https://doi.org/10.1016/j.soilbio.2020.108113.
Tian, D., Niu, S., 2015. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10, 024019. https://doi.org/10.1088/1748-9326/10/2/024019.
Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., Polasky, S., 2002. Agricultural sustainability and intensive production practices. Nature 418, 671–677. https://doi.org/10.1038/nature01014.
Tkacz, A., Bestion, E., Bo, Z., Hortala, M., Poole, P.S., 2020. Influence of plant fraction, soil, and plant species on microbiota: a multikingdom comparison. mBio 11 (1), e02785-19. https://doi.org/10.1128/mbio.02785-19.
Tosi, M., Deen, W., Drijber, R., Mcpherson, M., Dunfield, K., 2021. Long-term N inputs shape microbial communities more strongly than current-year inputs in soils under 10-year continuous corn cropping. Soil Biol. Biochem. 160, 108361. https://doi.org/10.1016/j.soilbio.2021.108361.
Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T., Singh, B.K., 2020. Plant-microbiome interactions: from community assembly to plant health. Nat. Rev. Microbiol. 18, 607–621. https://doi.org/10.1038/s41579-020-0412-1.
Wang, R., Dorodnikov, M., Shan, Y., Zhang, Y., Yong, J., 2015. Responses of enzymatic activities within soil aggregates to 9-year nitrogen and water addition in a semi-arid grassland. Soil Biol. Biochem. 81, 159–167. https://doi.org/10.1016/j.soilbio.2014.11.015.
Wang, Q., Jiang, X., Guan, D., Wei, D., Zhao, B., Ma, M., Chen, S., Li, L., Cao, F., Li, J., 2018c. Long-term fertilization changes bacterial diversity and bacterial communities in the maize rhizosphere of Chinese mollisols. Appl. Soil Ecol. 125, 88–96. https://doi.org/10.1016/j.apsoil.2017.12.007.
Wang, L., Luo, X., Liao, H., Chen, W., Wei, D., Cai, P., Huang, Q., 2018b. Ureolytic microbial community is modulated by fertilization regimes and particle-size fractions in a black soil of northeastern China. Soil Biol. Biochem. 116, 171–178. https://doi.org/10.1016/j.soilbio. 2017.10.012.
Wang, J., Song, Y., Ma, T., Waseem, R., Li, J., Jillian, H., Huang, Q., Shen, Q., 2017. Impacts of inorganic and organic fertilization treatments on bacterial and fungal communities in a paddy soil. Appl. Soil Ecol. 112, 42–50. https://doi.org/10.1016/j.apsoil.2017.01.005.
Wu, M., Qin, H., Zhe, C., Wu, J., Wei, W., 2011. Effect of long-term fertilization on bacterial composition in rice paddy soil. Biol. Fertil. Soils 47 (4), 397–405. https://doi.org/10.1007/s00374-010-0535-z.
Wang, C., Wu, S., Moussa, T., Zhang, X., Li, L., Gong, D., Hao, W., Mei, X., Wang, Y., 2018a. Stomatal aperture rather than nitrogen nutrition determined water use efficiency of tomato plants under nitrogen fertigation. Agric. Water Manag. 209, 94–101. https://doi.org/10.1016/j.agwat.2018.07.020.
Wu, L., Jiang, Y., Zhao, F., He, X., Yu, K., 2020. Increased organic fertilizer application and reduced chemical fertilizer application affect the soil properties and bacterial communities of grape rhizosphere soil. Sci. Rep. 10, 9568. https://doi.org/10.1038/s41598-020-66648-9.
Xu, L., Zhu, B., Li, C., Yao, M., Li, X., 2020. Development of biological soil crust prompts convergent succession of prokaryotic communities. Catena 187, 104360. https://doi.org/10.1016/j.catena.2019.104360.

Yang, X., Ni, K., Shi, Y., Yi, X., Zhang, Q., Fang, L., Ma, L., Ruan, J., 2018a. Effects of long-term nitrogen application on soil acidification and solution chemistry of a tea plantation in China. Agric. Ecosyst. Environ. 252, 74–82. https://doi.org/10.1016/j.agee.2017.10.004.

Yang, Y., Wang, Z., Zeng, Z., 2018b. Effects of long-term different fertilization and irrigation managements on soil bacterial abundance, diversity and composition. Sci. Agric. Sin. 51 (2), 290–301. https://doi.org/10.3864/j.issn.0578-1752.2018.02.009.

Ye, G., Lin, Y., Liu, D., Chen, Z., Luo, J., Bolan, N., Fan, J., Ding, W., 2019. Long-term application of manure over plant residues mitigates acidification, builds soil organic carbon and shifts prokaryotic diversity in acidic ultisols. Appl. Soil Ecol. 133, 24–33. https://doi.org/10.1016/j.apsoil.2018.09.008.

Zhalnina, K., Dias, R., Quadros, P.D.D., Davis-Richardson, A., Camargo, F.A.O., Clark, I.M., Mcgrath, S.P., Hirsch, P.R., Triplett, E.W., 2015. Soil pH determines microbial diversity and composition in the park grass experiment. Microb. Ecol. 69, 395–406. https://doi.org/10.1007/s00248-014-0530-2.

Zhang, X., Wei, H., Chen, Q., Han, X., 2014. The counteractive effects of nitrogen addition and watering on soil bacterial communities in a steppe ecosystem. Soil Biol. Biochem. 72, 26–34. https://doi.org/10.1016/j.soilbio.2014.01.034.

Zhang, Y.J., Hu, H.W., Chen, Q., Singh, B.K., Yan, H., Chen, D., He, J.Z., 2019. Transfer of antibiotic resistance from manure-amended soils to vegetable microbiomes. Environ. Int. 130, 104912. https://doi.org/10.1016/j.envint.2019.104912.

Zhou, J., Xia, F., Liu, X., He, Y., Xu, J., Brookes, P., 2014. Effects of nitrogen fertilizer on the acidification of two typical acid soils in South China. J. Soils Sediments 14, 415–422. https://doi.org/10.1016/j.agee.2017.10.004.

Zhou, J., Guan, D., Zhou, B., Zhao, B., Ma, M., Qin, J., Jiang, X., Chen, S., Cao, F., Shen, D., Li, J., 2015. Influence of 34-years of fertilization on bacterial communities in an intensively cultivated black soil in northeast China. Soil Biol. Biochem. 90, 42–51. https://doi.org/10.1016/j.soilbio.2015.07.005.