



Balancing water efficiency and crop productivity: rhizosphere microbiome shifts in drought-resistant rice

Junguo Bi¹ · Jiayi Li² · Saeed ur Rahman² · Yuchong Long² · Nan Hui^{3,4,5} · Martin Romantschuk⁶ · Junqiang Zheng^{7,8} · Xianxian Zhang¹ · Danping Hou¹ · Jinsong Tan¹ · Qingyu Bi¹ · Hui Xia¹ · Xinqiao Yu¹ · Lijun Luo¹ · Xinxin Liu²

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Abstract

Water-saving and drought-resistant rice (WDR) is a type of cultivated rice (*Oryza sativa* L.) developed to maintain yield under water-scarce conditions. The rhizosphere microorganisms play a crucial role in regulating plant growth and improving soil conditions. However, the microbial communities present in the rhizosphere of WDR have been inadequately characterized. In this study, we conducted a comparative analysis of soil microbial communities in drought-resistant rice Hanyou73 (HY73), upland rice Baishahan (BS), and wetland rice Huanghuazhan (HH) in May and October. Two irrigation regimes and 30 blocks (3 m x5 m each) were set up in the field: full water irrigation, and 50% water irrigation. Our findings revealed that the yield of HY73 was 64.71% and 50.41% higher than that of HH and BS under 50% water irrigation, respectively. Additionally, we observed a positive correlation between the water content and both ammonia nitrogen and nitrate nitrogen (NN) in soil. Moreover, phosphorus availability was strongly influenced by soil pH. Furthermore, microbial communities were characterized via high-throughput DNA sequencing. The diversity of the rhizosphere microbial community was reduced under 50% water irrigation. In October, soil NN levels were higher under 50% water irrigation than under full water irrigation. Under condition of 50% water irrigation, the NN levels in HY73 soil were 7.8% lower compared to HH, and 22.0% lower than BS. Rice yield was positively correlated by Proteobacteria, Chloroflexi, Gemmatimonadetes, and Ascomycota. An increase in ammonia-oxidizing bacteria was observed during the tillering stage, especially in the soils of HY73. These findings provide insights into the role of rhizosphere microorganisms in enhancing the drought resistance and yield potential of water-saving rice varieties, which may contribute to the development of sustainable agricultural practices in water-limited regions.

Keywords Water-saving and drought-resistant rice (WDR) · Rhizosphere microbiome · Sustainable agriculture · Microbial ecology

Junguo Bi, Jiayi Li and Saeed ur Rahman contributed equally.

✉ Lijun Luo
lijun@sagc.org.cn

✉ Xinxin Liu
xinxin.liu@sjtu.edu.cn

¹ Shanghai Agrobiological Gene Center, Shanghai 201106, China

² School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai 200240, China

³ Key Laboratory of Urban Agriculture, School of Agriculture and Biology, Shanghai Jiao Tong University, Shanghai 200240, China

⁴ Shanghai Yangtze River Delta Eco-Environmental Change and Management Observation and Research Station, Ministry of Science and Technology, Ministry of Education, 800 Dongchuan Rd, Shanghai 200240, China

⁵ Shanghai Urban Forest Ecosystem Research Station, National Forestry and Grassland Administration, 800 Dongchuan Rd, Shanghai 200240, China

⁶ Faculty of Biological and Environmental Sciences, University of Helsinki, Niemenkatu 73, Lahti 15140, Finland

⁷ International Joint Research Laboratory for Global Change Ecology, School of Life Sciences, Henan University, Kaifeng, Henan 475004, China

⁸ Yellow River Floodplain Ecosystems Research Station, School of Life Sciences, Henan University, Xingyang, China

Introduction

Rice (*Oryza sativa* L.) production is the largest consumer of freshwater in China, accounting for 70% of the country's total groundwater withdrawals (Bi et al. 2021; Xu et al. 2015). In response to the water crisis, sustainable rice production has focused on developing water-saving and drought-resistant rice (WDR) varieties, such as Hanyou73 (Bi et al. 2021), which can achieve a similar grain yield to wetland rice while reducing water consumption by up to 50%; however, the specific environmental factors that contribute to sustaining this yield under drought conditions are largely unknown.

The response of roots to water stress greatly depends on the crop genotype, growth stage, and intensity of stress (Xu et al. 2015). The drought tolerance capacity of rice is typically determined by the presence and efficiency of drought-adaptation mechanisms encoded in its genome (Oladosu et al. 2019). For instance, the overexpression of the late embryogenesis abundant (LEA) gene *OsLEA3-1* in rice has been reported to play a significant role in drought tolerance and in reducing yield loss under severe drought conditions (Nurdiani et al. 2018). Overexpression of zinc finger proteins OsZFP252 has also been shown to enhance drought tolerance by increasing soluble sugar and proline accumulation, resulting in a 74–79% higher survival rate (Xu et al. 2008). Additionally, WDR varieties are characterized by a low root biomass and high root absorption efficiency, allowing them to maintain more dry material in the aboveground parts by reducing the root-to-shoot ratio (Bi et al. 2021), which highlights their water-saving and drought-tolerant attributes, emphasizing the genetic and physiological traits inherent in these rice cultivars; however, further research is needed to fully understand these mechanisms.

The microbial community and diversity changes in the rhizosphere are primarily influenced by factors such as plant type and soil physicochemical properties (Khalid et al. 2023b; ur Rahman et al. 2025a; Rahman et al. 2025b). These changes play a crucial role in shaping the soil microbiome and its interactions with plants. Some plant roots secrete specific organic substances that attract certain microbes, such as Rhizobia on legumes or matching arbuscular mycorrhizae on rice (Wang et al. 2023; Yang et al. 2015). Drought stress alters the development of root-associated microbiomes by shifting soil physicochemical characteristics. For instance, conversions from dryland to wetland rice cultivation have been shown to affect soil carbon cycling and the number of fungal amplicon sequence variances (ASVs) (Li et al. 2021). Anaerobic genera *Desulfovibrio*, *Geobacter*, and *Anaeromyxobacter* are often depleted by drought (Santos-Medellín et al. 2017). Various studies have shown a clear link between the presence of microbial communities and the enhancement of plant growth, particularly in terms

of drought resilience. Certain members of Acidobacteria are closely related to rice yield as they efficiently degrade cellulose and regulate soil pH (García-Orenes et al. 2016). Soil fertility is another key driver of local adaptation in arbuscular mycorrhizal (AM) symbioses, and nutritional mutualisms play a critical role in environments with strongly limiting soil phosphorus availability (Cheeke et al. 2017). Conversely, Chloroflexi are green non-sulfur bacteria that are unable to fix nitrogen (Dotaniya and Meena 2015) and could potentially compete with crops for nitrogen nutrients. The gap in understanding the relationship between the rhizosphere microorganisms of water-saving drought-resistant rice and rice yield impedes progress in enhancing rice productivity and effective soil management strategies.

Among the various soil nutrient cycles mediated by microorganisms, the nitrogen cycle is paramount for plant growth, and shifts in the microbial community are known to directly alter nitrogen transformation processes. Nitrogen (N) is an essential nutrient for rice plants and is the most limiting nutrient for rice production (Ladha et al. 2016). Inorganic N is the main N form directly absorbed by rice, but only accounts for approximately 1% of the total N in the soil, being produced mainly from mineralization in the soil (Chunmei et al. 2020). The dynamics of nitrogen in agroecosystems are complex, influenced by a multitude of factors, including irrigation management. For instance, (Cheng et al. 2022) demonstrated that alternating wetting and drying irrigation can significantly alter the speciation of nitrogen, affecting its availability to rice plants. The interplay between water management practices and these nitrogen forms is a critical determinant of rice plant nitrogen uptake and utilization (Cheng et al. 2022). Therefore, nitrogen supply in soil is often one of the main factors limiting crop yield and food quality (Dotaniya and Meena 2015).

In this study, the microbial communities under two irrigation methods (50% water irrigation and full water irrigation) and three rice varieties (WDR, upland rice, and wetland rice) were investigated using high-throughput DNA sequencing. Given that soil N metabolism is more active in drought-resistant rice than in wetland rice (HongYing et al. 2017). The rhizosphere microbiota and their N-related functions likely explain rice yield under drought stress (Abdou et al. 2021). We hypothesize that the high yields of the WDR variety HY73 under drought conditions can be attributed to its unique rhizosphere microbial community, which is characterized by an enhanced abundance of ammonia-oxidizing bacteria. This study aims to fill a critical knowledge gap by directly linking the unique rhizosphere microbiome of a high-performing WDR variety to its nitrogen-cycling functions and yield sustainability under water-saving irrigation, an area that remains underexplored despite the agronomic importance of WDR cultivars. Furthermore, the microbial

and biochemical changes under 50% water irrigation led to improved nitrogen uptake and utilization, ultimately resulting in a higher grain yield in WDR.

Materials and methods

Site description and plant materials

The experiments were carried out from May to October in 2022 at the Zhuanghang Experimental Station (30°53'10"N, 121°38'51"E), Shanghai Academy of Agricultural Sciences, Fengxian, Shanghai, China. Three rice varieties were evaluated, namely a water-saving and drought-resistant rice Han-you73 (HY73); upland rice Baishahan (BS); and a wetland rice Huanghuazhan (HH). The rice seeds were kindly provided by Prof. Junguo Bi from Shanghai Academy of Agricultural Sciences.

Experimental design

The experimental field was 25 m long and 18 m wide, and it was evenly divided into 30 blocks (3 m x 5 m), using a random block design. All blocks were located outdoors (Fig. 1a and b). The treatments started from May and ended in October 2022. There were two irrigation regimes: the full water irrigation (RI) and the water-saving irrigation (WS), which received 50% of the volume applied to the RI plots. The irrigation volume was manually controlled using a flow meter installed at the water source.

The RI treatment maintained a 2–3 cm standing water layer, which was monitored and recorded every 48 h using a graduated staff gauge installed in each RI plot. Water was added to restore the level to 3 cm whenever it fell below 2 cm.

The WS treatment received no standing water. Irrigation was triggered when the soil surface showed visible cracking and the average soil moisture content in the top 20 cm, as measured by a time-domain reflectometry (TDR) probe,

dropped below 60% of field capacity. The volume of water applied was precisely controlled to equal 50% of the amount used in the RI treatment during the same period, as verified by the flow meter. Each irrigation treatment was imposed at the same time in five replicates. To ensure the uniformity of the seedlings, rice seeds were pregerminated and then grown in test fields. A compound fertilizer (2.5 g N: P₂O₅: K₂O=15:15:15) was applied to the field, and 1 kg of urea was applied at the tillering stage. All seedlings were well watered before the beginning of the experimental treatments.

Soil sampling and edaphic conditions

We sampled soils once a month from May to October 2022, in total 6 times representing (i) seeding stage (May), (ii) tillering stage (June), (iii) jointing and elongation stage (Jul.), (iv) booting and heading stage (Aug.), (v) grain filling and maturity stage (Sep.) and (vi) recovery stage (Oct.). At each sampling point, 10 rice plants were randomly taken from each field block for rhizosphere soil collection. Soils from the each 10 plants were mixed well into one Minigrip bag consist one sample. All of the samples were kept on dry ice in the field until being frozen at –20 °C in the laboratory. The samples were thawed at room temperature (for chemical analyses) and at +4 °C (for DNA analyses), and sieved, using 2 mm mesh size, to remove stones, roots and large particles. Edaphic conditions were determined for all samples. Soil pH was measured by adding 2 g of soil into 20 ml of 0.01 M CaCl₂. The soil water content (WC) was determined by the wet-dry specific gravity method. The electrical conductivity (EC) of the soil was measured by EC meter. TC and TN were determined by dry combustion at 1350 °C using a LECO CNS-2000 Elemental Analyzer (0.07% C and 0.09% N detection limits) (Dutta et al. 2024). After wet digestion with H₂SO₄ and HClO₄, total phosphorus (TP) and total potassium (TK) were determined colorimetrically by Lachat QuikChem AE Flow-injection Autoanalyzer, respectively (Foreman et al. 2024).

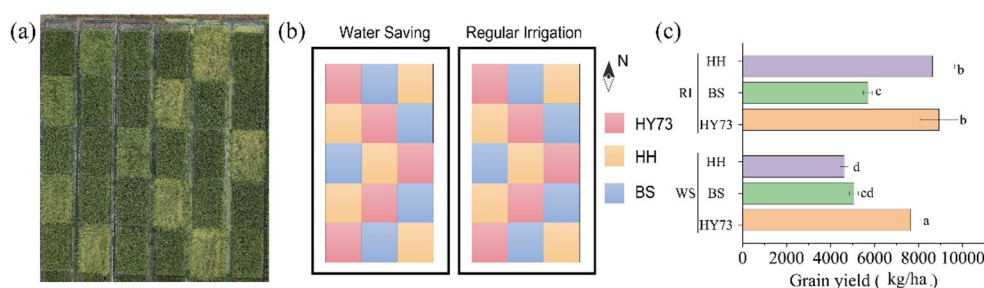


Fig. 1 Planting distribution map. (a) field photograph; (b) experimental design pattern map; (c) the effect of different irrigation treatments on the grain yield of HY73, BS and HH. In (b), the red, yellow and blue blocks represent HY73, BS and HH, respectively. In (c), the yellow, green and purple bars represent HY73, BS and HH, respectively. WS:

50% water irrigation, RI: full water irrigation. Values are means $\pm$ SDs ($n=5$). Statistical significance was analyzed using paired Student's *t*-tests. Duncan's analysis indicated a significant difference ($p<0.05$) among the groups. Similarly, in subsequent analyses significant differences were observed for the variables under investigation ($p<0.05$)

Measurement of rice growth and yield components

Ten homogenous rice plants were selected from each treatment at maturity, to determine the effects of the irrigation treatments on yield in HY73, BS and HH. This was achieved by measuring the spike number, grain number per spike, and seed setting rate (stem and tiller panicle rate calculated as highest tiller number/final panicle number $\times$ 100%), and dry grain weight of 5 randomly selected plants. The remaining 5 plants were used for estimating the grain yield per plant, which was adjusted to account 14% grain moisture content. During mid-tillering, panicle initiation, heading, and maturity growth stages, three intact plants from each treatment were gently pulled out and separated into panicle, leaf, culm, and leaf sheaths and roots. The organs were oven-dried at 70 °C to constant weight, and the final oven-dry weight of the samples was recorded (Digital display oven dryer WHL-30 Tianping Shanghai). Total dry matter weight in panicles, leaves, stems (culms and sheaths), and roots of mature rice plants was measured to determine the effects of irrigation treatments (Wang et al. 2022).

DNA extraction, PCR and illumina miseq sequencing

The soil samples were homogenized in liquid nitrogen and mixed completely, and 10 g (8.2–10.1 g fresh weight) of each soil sample was used for DNA extraction by using the PowerMax Soil DNA Isolation Kit (MoBio, Carlsbad, California) following the manufacturer's instructions. The hypervariable region (V3 and V4) of the bacterial 16S rRNA gene was amplified by primers 515F 5'-GTGCCAGCMGC-CGCGGTAA-3' and 806R 5'-GGACTACHVGGGTC-TAAT-3'. For ITS amplification, a similar approach was employed using the primers fITS7 5'-GTGARTCATC-GAATCTTTG-3' and ITS4 5'-TCCTCCGCTTATTGATA TGC-3'. In the secondary PCR, the full-length P5 adapter and indexed P7 adapter were used. The DNA samples were analyzed using the Fragment Analyzer (Advanced Analytical, USA) and the amplicons were sequenced with Illumina MiSeq (v.3 2 $\times$ 300 bp paired-end) at the Institute of Biotechnology, University of Helsinki, Finland. Both bacterial and fungal paired fastq files are available in the Sequence Read Archive at NCBI (www.ncbi.nlm.nih.gov) under BioProject numbers PRJNA1036150 and PRJNA1027973, respectively.

Bioinformatics

The paired-end sequence data (.fastq) were processed using Mothur (version 1.36.1). Both bacterial and fungal fastq files were integrated, and any sequences with ambiguous bases, multiple mismatches with primer aggregates,

homopolymers larger than 8 bp, and any sequences without a minimum overlap of 50 bp were removed. As a result, a total of 8,203,287 bacterial sequences and 7,503,158 fungal sequences were obtained.

Bacterial sequences were aligned with the Silva reference, pre-clustered to remove erroneous reads (Huse et al. 2010), and screened for chimeras with the Vsearch algorithm (Edgar et al. 2011). Non-chimeric sequences were then assigned to taxa using the naïve Bayesian classifier (Wang et al. 2007) with the RDP training set for bacteria and UNITE database for fungi. Non-target sequences (mitochondria, chloroplasts, archaea) were removed, and the data were rarefied before computing diversity indices. Sequences were assigned into amplicon sequence variance (ASV). All fungal ASVs were classified into functional guild using the FUNGuild database (Huse et al. 2010).

Statistical analysis

All statistical analyses were performed in R (version 4.3.1) (Grunsky 2002). All data are expressed as the means $\pm$ standard deviations (SDs). Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities, carried out using the vegan package (v. 2.6–4.6), was used to visualize the bacterial and fungal communities. Permutational multivariate analysis of variance (PERMANOVA) with 999 permutations was used to test the significance of grouping factors in the NMDS ordination.

Two-way ANOVA was used to ascertain the influence of irrigation treatments and rice varieties on rice growth, edaphic conditions, diversity indices and relative abundances of taxonomic groups. When a significant interaction or main effect was found ($p \leq 0.05$), post-hoc pairwise comparisons were conducted using Tukey's Honest Significant Difference (HSD) test. The topology of the network map was used to identify the key species in this microbial community (Kim et al. 2021). Differences between treatments were considered statistically significant at $P \leq 0.05$.

Results

Water-saving irrigation significantly reduces grain yield across rice cultivars

The results indicated that water-saving (WS) irrigation had a significant negative effect ($p < 0.05$) on the grain yield of both HY73 and HH cultivars (Fig. 1c). The impact of drought on BS was less pronounced, but still resulted in lower yield and yield components when compared to HY73 under both WS and regular irrigation (RI)

conditions. The different irrigation treatments had varying effects on the yield components of the cultivars. Among the three varieties, HY73 achieved the highest yield (8929.5 kg/ha) in the waterlogged field. However, in the WS field, the yield of HY73 decreased to 7641.0 kg/ha. HH had a similar grain yield to HY73 under full water irrigation, but the yield significantly decreased in the WS, with a grain yield of 4621.5 kg/ha. The yield of BS grain was 5694.0 kg/ha in RI, which was lower than that of HH and HY73 (Fig. 1c).

Irrigation method strongly influences soil properties, with minor varietal effects

Soil properties were mainly influenced by irrigation methods, with rice varieties having a comparatively minor impact. Soil pH varied from 6.40 to 7.70 over the growing season (Fig. 2). 50% water irrigation had minor effects on soil pH and OM, while the pH of BS and HH declined in RI (Fig. 2). Water content decreased after a growing period of rice, especially in WS (Fig. 2). On the contrary, EC increased (Fig. 2b). In May, TN, NN, and AN were similar. By October, TN remained at levels similar to those in May, but NN was significantly higher in WS than in others treatments ($p < 0.001$), ranged from 13.14 mg/kg in HY73 soil to 16.86 mg/kg in BS soil (Fig. 2). AN, TP and AP decreased in October. AN and TP in WS were lower, while AP showed an opposite trend (Fig. 2e).

Microbial community composition and structure respond to irrigation treatments

Water-saving irrigation increases microbial richness and diversity, especially among bacteria

The microbial community shifted after the growing period between RI and WS, but showed little difference among HY73, HH and BS (Fig. S2). 50% water irrigation increased the richness, diversity and evenness of microbial community. This effect was more pronounced in bacteria than in fungi.

Bacterial community structure and functions shift under water-saving irrigation

The bacterial sequences were clustered into 28,074 ASVs and assigned into 55 phyla, 177 classes, 343 orders, 459 families, and 610 genera (Table. S1). Overall, bacterial communities were dominated by Proteobacteria (36.18%), Acidobacteria (18.17%), Chloroflexi (13.16%), Actinobacteria (7.88%), Firmicutes (3.52%), Gemmatimonades (3.92%), Planctomycetes (3.40%), Nitrospirae (3.15%), Bacteroidetes (2.63%), Verrucomicrobia (1.98%), accounting for 93.99% of the sequences (Table S1). A vast majority, 99.03% of the sequences were common in both irrigation treatments, and 81.10% were common across all 3 rice varieties. Notably, among the dominant phyla, Proteobacteria and Bacteroidetes showed pronounced differences between different irrigation methods (Fig. 2). Most bacterial genera

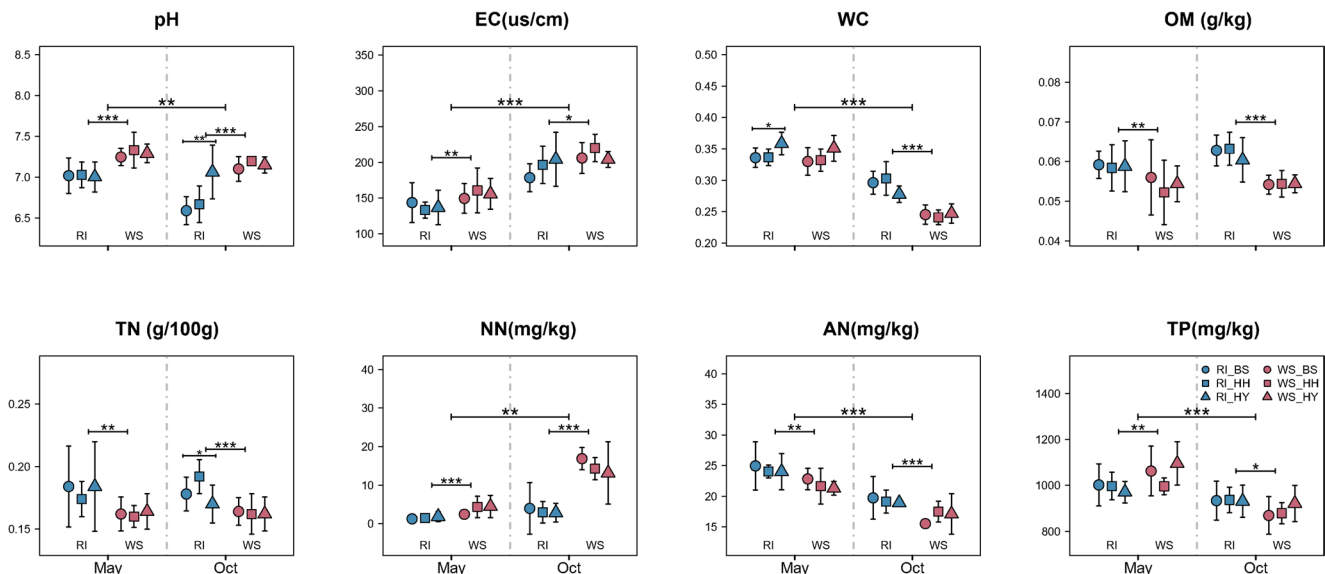


Fig. 2 Physical and chemical characteristics of soil in May and October. (a) pH (b) EC, electrical conductivity (c) WC, water content (d) TN, total nitrogen (e) AN, ammoniacal nitrogen (f) NN, nitrate nitrogen. The yellow, green and purple bars represent HY73, BS and HH, respectively. Values are means $\pm$ SDs ($n = 5$ biological replicates). Sta-

tistical significance was analyzed using paired Student's t-tests. Duncan's analysis indicated a significant difference ($p < 0.05$) among the groups. Similarly, in subsequent analyses, significant differences were observed for the variables under investigation ($p < 0.05$)

were dominated by *Kaistobacter* (1.62%), *Clostridium* (1.54%), *Geobacter* (0.98%), *Anaeromyxobacter* (0.92%), and the remaining were unclassified.

Generally, bacterial communities were dominated by chemoheterotrophy (22.53%), nitrification (16.13%), aerobic nitrite oxidation (15.96%), aerobic chemoheterotrophy (17.69%), fermentation (4.61%), iron respiration (5.29%), respiration of sulfur compounds (2.79%), sulfate respiration (2.77%), dark sulfide oxidation (1.49%) and dark oxidation of sulfur compounds (1.49%) according to function type. All types showed differences across the rice growing period ($p < 0.001$) (Fig. 3). Chemoheterotrophy had the highest abundance across all samples. Nitrification and aerobic nitrite oxidation bacteria were observed to become more abundant in WS during the tillering stage and showed difference between HY73 and HH ($p < 0.01$).

Fungal community composition and functional traits vary with irrigation but not rice variety

Fungal ASVs were represented by communities from 8 phyla, 34 classes, 94 orders, 202 families, and 362 genera. Out of the 7,779 fungal ASVs, 75.85% were found common in both irrigation methods and 40.60% were common across all 3 rice varieties (Fig. 4, Table. S2), showing more variation compared to bacteria. Generally, the dominant phyla were Ascomycota (63.05%), Zygomycota (7.06%), Basidiomycota (2.91%), Glomeromycota (0.32%), Rozellomycota (0.18%) and Chytridiomycota (0.13%). Among the most abundant 6 phyla, Ascomycota and Zygomycota showed significant differences between the 2 irrigation methods ($p < 0.05$, Fig. 4). The most abundant genera were *Mortierella* (6.95%) and *Fusarium* (6.58%).

According to function distinction, fungi were classified as Saprotroph (45.76%), Pathotroph-Saprotroph-Symbiotroph (27.26%), Saprotroph-Symbiotroph (18.69%), Pathotroph (6.43%), Symbiotroph (0.84%) and Pathotroph Saprotroph (0.67%). These functional categories showed pronounced differences across the rice growing period ($p < 0.001$, Fig. 5). Saprotroph and Pathotroph-Saprotroph-Symbiotroph fungi had the highest frequencies, which mainly contributed to the differences in fungal communities ($p < 0.05$). Rice varieties and irrigation type had minor effect on the fungal functional traits.

Soil moisture and pH are major drivers of microbial community structure under different irrigation regimes

Rhizosphere bacterial communities appeared to differ between water saving (WS) and regular irrigation (RI) treatments ($R^2 = 0.129$, $p = 0.001$, Fig. 6a) and among rice varieties ($R^2 = 0.081$, $p = 0.002$, Fig. 6b). pH ($R^2 = 0.132$, $p = 0.001$)

was the most predominant environmental factor driving bacterial community structure, followed by water content (WC) ($R^2 = 0.116$, $p = 0.001$). Similarly, fungal communities were also shaped by irrigation treatments ($R^2 = 0.040$, $p = 0.001$, Fig. 6c) and among rice varieties ($R^2 = 0.073$, $p = 0.001$, Fig. 6d). However, fungal community structures were mainly driven by WC ($R^2 = 0.150$, $p = 0.001$). These data suggest that rice with water saving irrigation, irrespective of rice varieties, does not approximate microbial communities in the fields with regular irrigation.

Specific bacterial and fungal taxa are positively correlated with rice yield under contrasting irrigation treatments

Evaluation of rice yield under two irrigation treatments and 3 rice varieties in 600 rice samples revealed that rice yield was positively influenced by Proteobacteria, Chloroflexi, Gemmatimonates and Ascomycota (Fig. 7). However, the correlation between rhizosphere microorganisms and rice yield varied with rice varieties. Proteobacteria, Chloroflexi, Gemmatimonates and Ascomycota promoted the yield of BS in both WS and RI conditions ($p < 0.05$). On the other hand, none of the rhizosphere microorganisms showed a significant association with HY73 yield. In contrast to BS, Proteobacteria, Chloroflexi, Gemmatimonates and Acidobacteria were strongly correlated with the yield of wetland rice HH under both irrigation methods. Additionally, the yield of grain with high water irrigation was promoted by Acidobacteria (in RI), while Rozellomycota promoted the yield under 50% water irrigation (in WS) (Fig. 7) ($p < 0.05$).

Co-occurrence networks reveal reduced microbial connectivity and stability under water-saving irrigation

Based on the Spearman correlation among ASVs, co-occurrence networks were constructed and analyzed for different groups (2 irrigation methods and 3 rice varieties) (Fig. 8). The results revealed significant differences ($p < 0.05$) in the topological structure characteristics of the network among the six groups. The network topology of bacterial and fungal networks fits the power-law distribution very well, suggesting that only a few nodes in the networks have a significantly higher number of linkages compared to the rest of the nodes in the networks. The nodes and links of co-occurrence networks declined from May to October. The co-occurrence network under regular irrigation (RI) was significantly larger and more complex, comprising 512 nodes and 1,845 links, compared to the water-saving (WS) network, which contained only 387 nodes and 1,102 links. Connections in October were all lower than those in May, indicating that rice cultivation resulted in reduced microbial stability in the rhizosphere (Fig. 9). Moreover, connections in WS were fewer

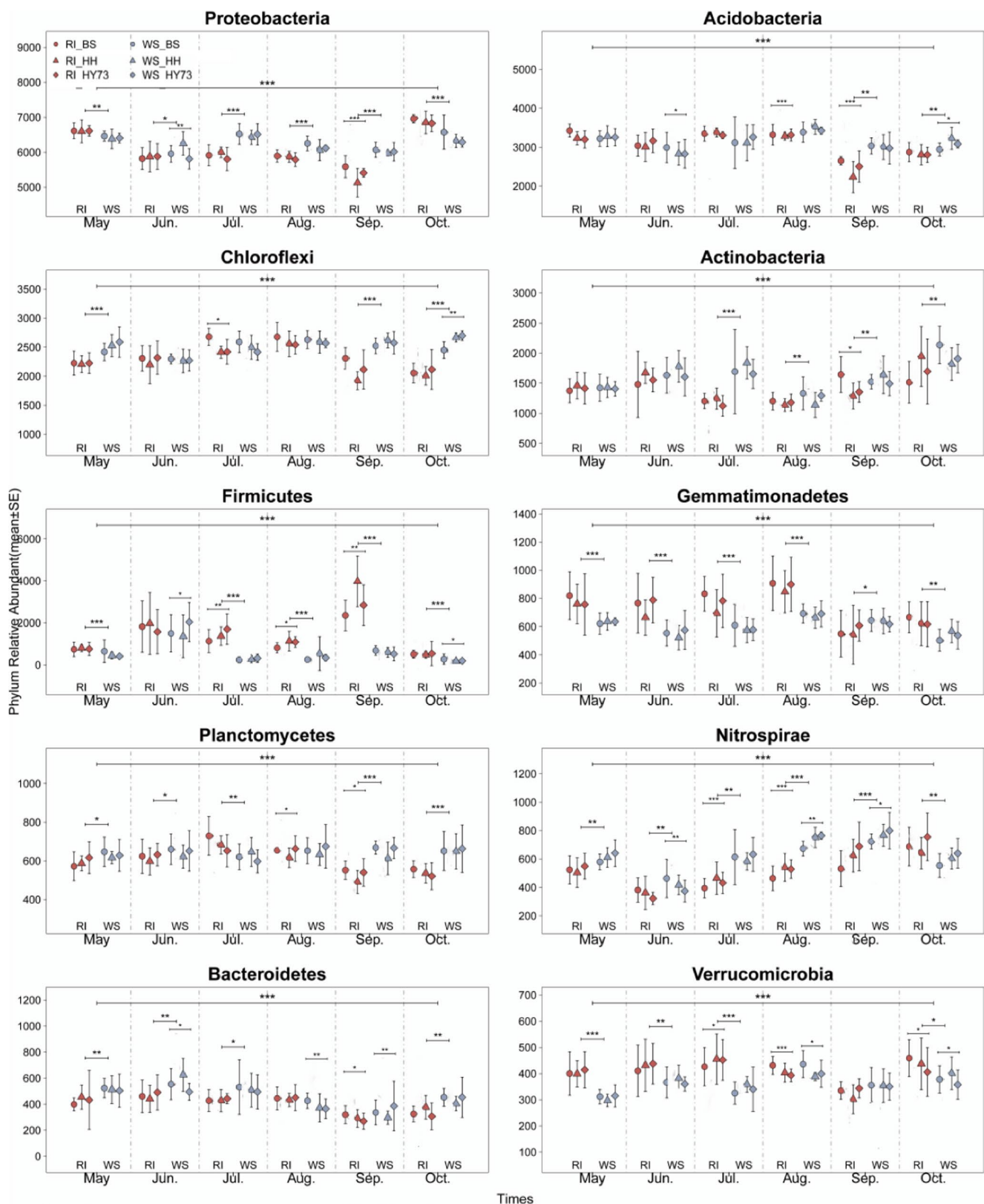


Fig. 3 The relative abundance response of the major bacterial phyla. The horizontal axis represents the planting time as well as the irrigation treatment. WS: water saving irrigation, RI: regular irrigation. The vertical axis represents the relative abundance in the number of sequence reads.

RI-BS indicates the BS group under regular irrigation, with other treatment group labels following a similar. Bars represent standard errors. “*” represents differences, where $p < 0.05$, “**” represents $p < 0.01$, and “***” represents $p < 0.001$. The same applies for the following

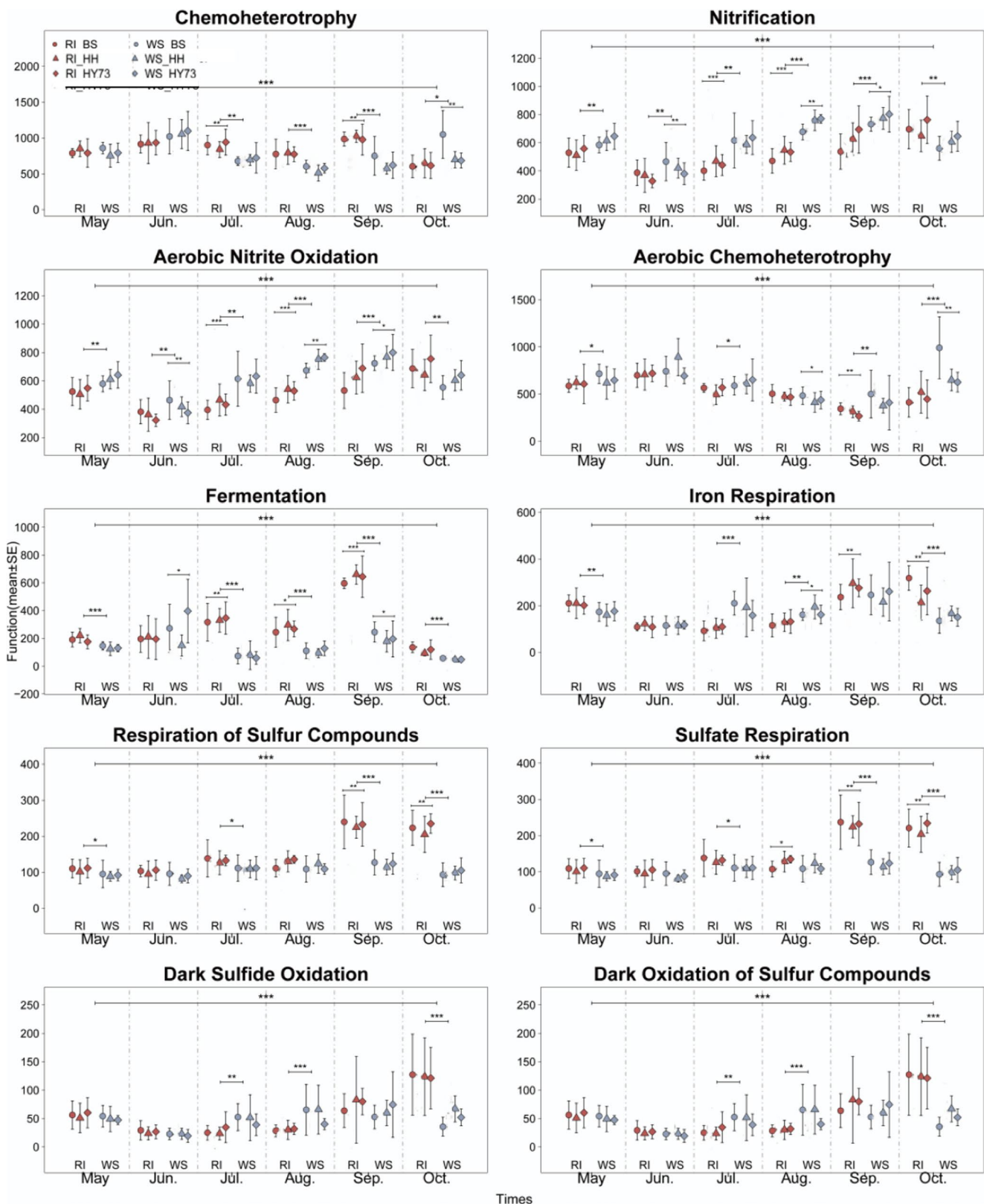


Fig. 4 Functional annotation of the main bacterial genera. The horizontal axis represents the planting time. WS: water saving irrigation, RI: regular irrigation. The vertical axis represents the relative abundance in the number of sequence reads. RI-BS indicates the BS group

under regular irrigation, with other treatment group labels following a similar pattern. Bars represent standard errors. “*” represents differences where p is <0.05 , “**” represents $p < 0.01$, and “***” represents $p < 0.001$. The same applies for the following

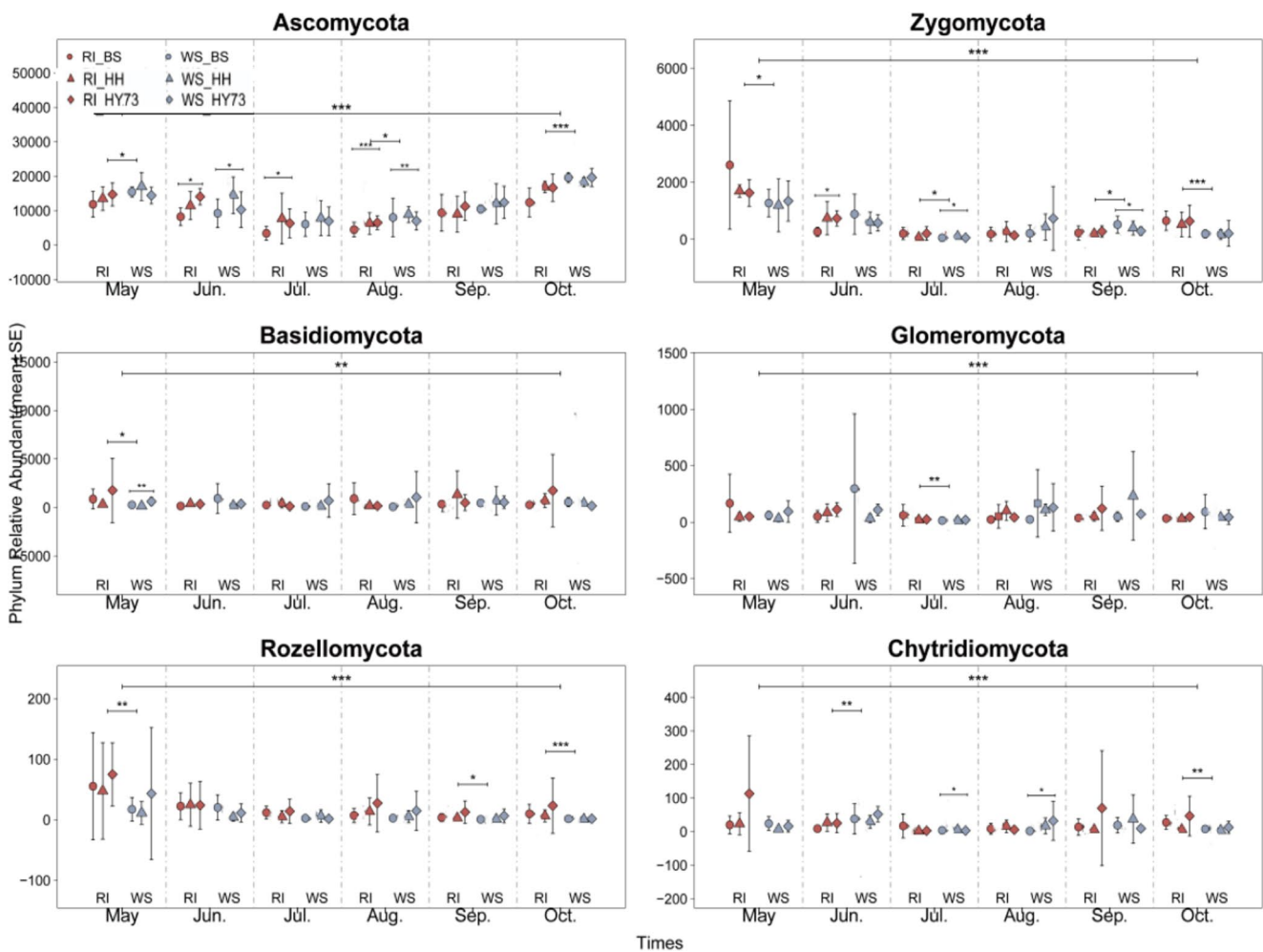


Fig. 5 Changes in the relative abundance of the major fungal phyla. The horizontal axis represents the planting time as well as the irrigation treatment. WS: water saving irrigation, RI: regular irrigation.

than those in RI, demonstrating that drought increased the instability of the rhizosphere microbial communities. The co-occurrence networks of BS exhibited more connectors than HY73 and HH in WS, possibly explaining the stability of BS grain yield in both IR and WS (Fig. S3). Proteobacteria and Ascomycota accounted for the majority of nodes, links, and topological roles, defined using the within-module connectivity (Z_i) and among-module connectivity (P_i). Specifically, nodes with $Z_i < 2.5$ and $P_i > 0.62$ are classified as network connectors. Chloroflexi exhibited more nodes and links in WS and WDR. After planting, Acidobacteria lost its status as a connector (Fig. S4).

Indicator taxa associated with drought-resistant cultivar HY73 highlight key bacterial and fungal responders

All together 43 bacterial indicator ASVs (Table. S1) and 16 indicator bacterial genera that showed significant differences

The vertical axis represents the relative abundance in the number of sequence reads. RI-BS indicates the BS group under regular irrigation, with other treatment group labels following a similar pattern

between the two irrigation treatments. Specifically, eight bacterial genera, *Pseudomonas*, *Pontibacter*, *Nitrospira*, *Planctomyces*, *Pirellula*, *Pedobacter*, *Solitalea* and *Caldilinea* were more common in the RI treatment compared to WS treatment ($p < 0.01$). Additionally, *Pseudomonas* and *Caldilinea* were less abundant in the HY73. Furthermore, 33 fungal indicator ASVs (Table. S2) and 16 fungal indicator genera were found between the 2 irrigation treatments. Among them, *Didymosphaeria*, *Cochliobolus* and *Myrothecium* were indicators of the HY73, with *Didymosphaeria* being enriched specifically in HY73.

Discussion

Drought stress often reduces rice yield as it limits soil moisture and reduces nitrogen uptake. With its ability to maintain a high-water status under drought through deep rooting

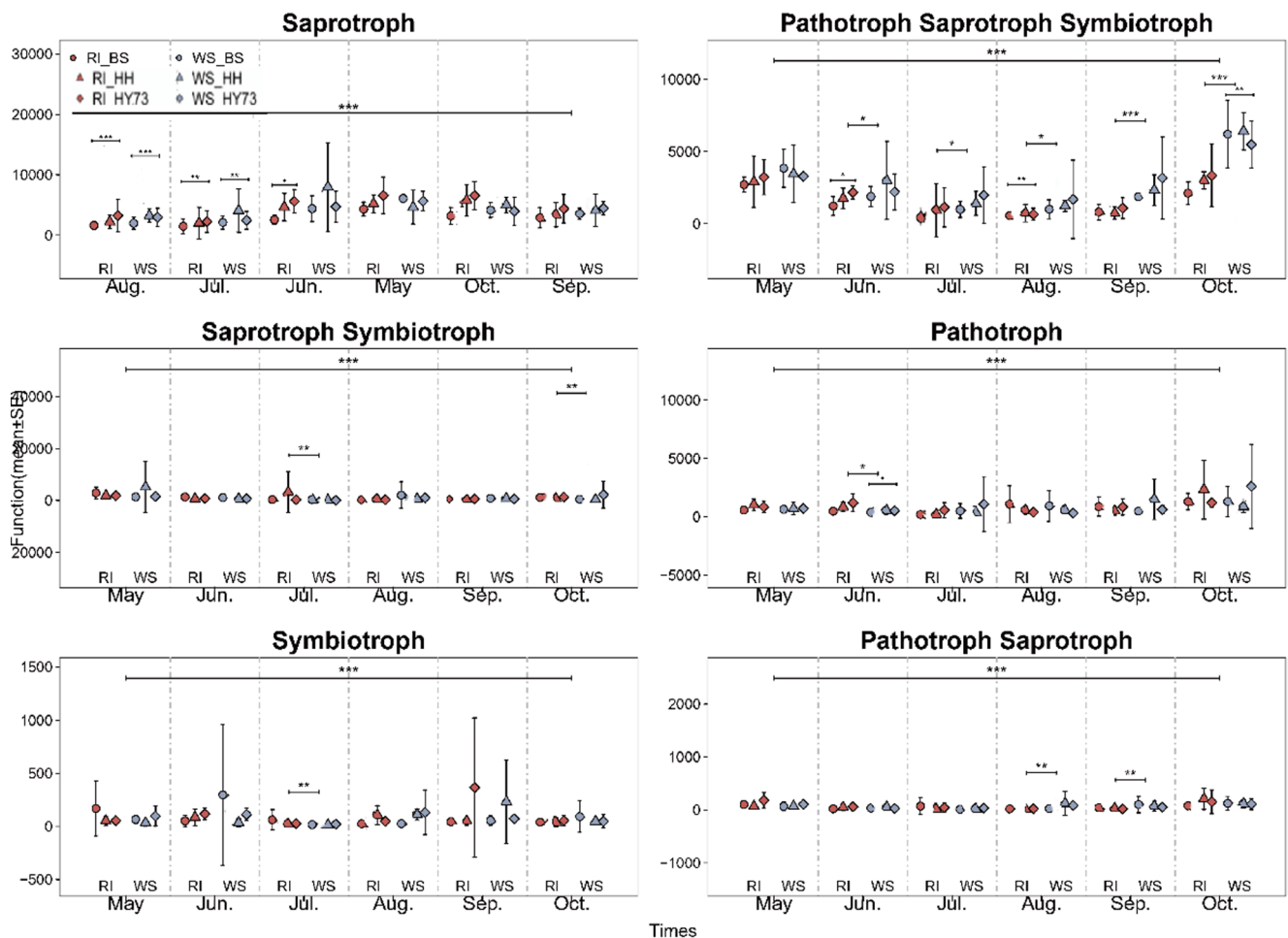


Fig. 6 Functional annotation of the major fungi. The horizontal axis represents the planting time as well as the irrigation treatment. WS: water saving irrigation, RI: regular irrigation. The vertical axis represents the relative abundance in the number of sequence reads. RI-BS

indicates the BS group under regular irrigation, with other treatment group labels following a similar pattern. Bars represent standard errors. “*” represents differences where $p < 0.05$, “***” represents $p < 0.01$, and “****” represents $p < 0.001$. The same applies for the following

and osmotic adjustment and anti-oxidation ability, WDR was able to maintain a higher grain yield compared to other varieties (Bi et al. 2021). Previous studies have shown that low water irrigation during the flowering stage strongly influences rice physiological traits and yield (Yang et al. 2016). However, when rice rhizosphere water was appropriately reduced, more nitrate was transported to the leaves and the yield was elevated (Jiao et al. 2018). The increased soil O_2 are beneficial to rice growth and the absorption and utilization of soil N, because rice can form a well-performing aerenchyma systems to alleviate most of the oxygen deprivation stress (Chunmei et al. 2020). In the current study, both HY73 and HH experienced a decrease in grain yield under 50% water irrigation, with HH showing a more significant reduction. These results are consistent with previous studies by Luo and Bi (Bi et al. 2021; Luo et al. 2019).

Nitrogen plays a critical role in rice yield. Since rice roots can excrete O_2 to the rhizosphere soil, the rhizosphere appears

as a mixture of AN and NN (AN is more common in flooded rice fields) (Xianglan et al. 2009). Nitrification involves the oxidation of ammonia to nitrite and nitrate, while denitrification occurs in anoxic conditions, leading to the production of N_2 rather than ammonia. Ammonification, on the other hand, converts organic nitrogen, such as proteins and urea, into ammonium ions (NH_4^+) under aerobic conditions. Consequently, levels of nitrate nitrogen would be expected to decrease as a result of flooding (Xiong et al. 2010). It is anticipated that 50% water irrigation creates an aerated soil environment, leading to an elevated nitrate nitrogen concentration in the soil. Partial nitrate nutrition can increase the nitrogen uptake by rice, particularly in varieties with high nitrogen use efficiency. Specifically, partial nitrate nutrition can adjust the photosynthetic characteristics of rice, particularly in varieties with different nitrogen use efficiencies. For instance, the presence of nitrate can increase the Rubisco content in rice varieties with high nitrogen use efficiency,

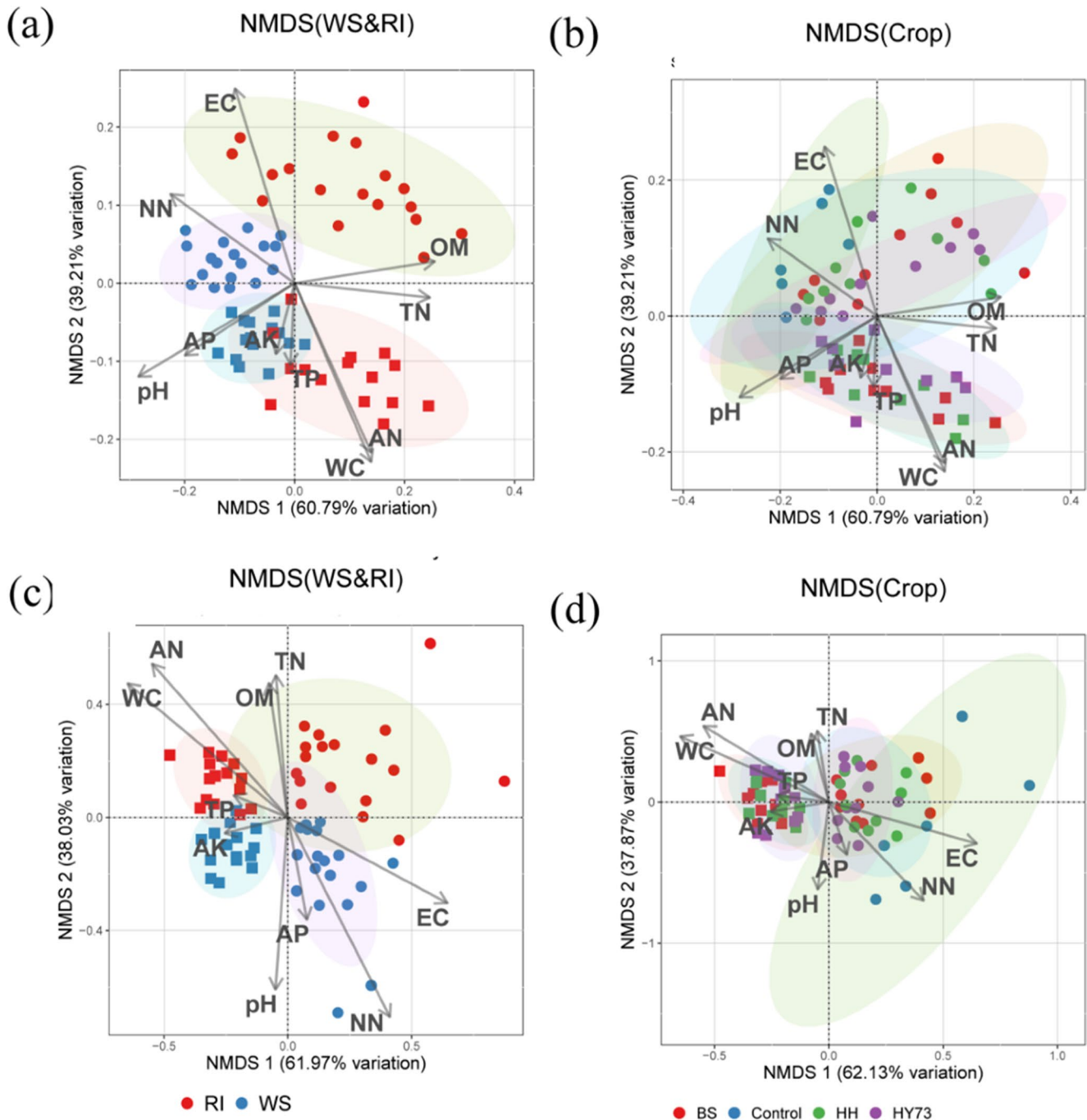


Fig. 7 The relationship between plant growth and rhizosphere microorganisms under three rice varieties and two irrigation conditions. The Mantel test analyzes the correlation between the microbes and the growth characteristics index of rice. Pearson correlation analysis mea-

sures the strength and direction of the linear relationship between two growth characteristics index of rice. The green line represents $P < 0.01$, red line represents $0.01 < P < 0.05$, and the blue line represents $P > 0.05$

which facilitates faster biomass accumulation during the late growth stages of rice (Zhang et al. 2011). In this study, NMDS analysis showed positive relationships between water content and available nitrogen. The research conducted by Xu et al. (Chunmei et al. 2020) revealed that NMDS analysis indicated a positive correlation between moisture levels

and accessible nitrogen. They discovered that employing a water-conserving irrigation technique while maintaining a constant nitrogen application rate led to enhanced levels of nitrogen-nitrate and available nitrogen in the soil. Additionally, they noted a more significant rise in NN, which aligns with the findings of the current investigation.

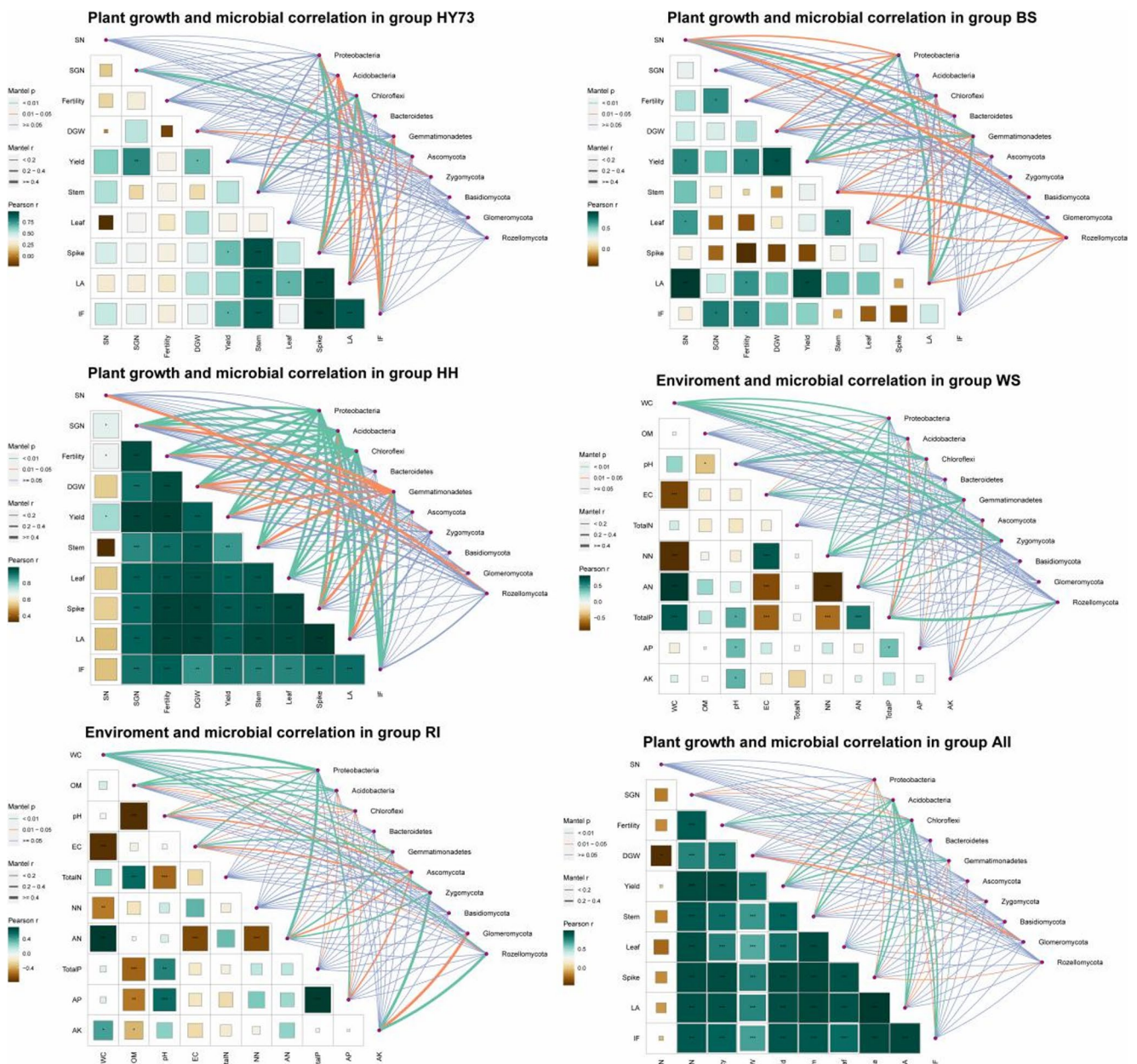


Fig. 8 The relationship between plant growth and rhizosphere microorganisms under three rice varieties and two irrigation conditions. The Mantel test analyzes the correlation between the microbes and the growth characteristics index of rice. Pearson correlation analysis mea-

sures the strength and direction of the linear relationship between two growth characteristics index of rice. The green line represents $P < 0.01$, red line represents $0.01 < P < 0.05$, and the blue line represents $P > 0.05$

Rice plants that exhibit a higher potential to inhibit nitrification processes may alter the microbial environment, particularly by affecting the ammonia-oxidizing bacteria populations which are key players in the conversion of ammonia to nitrite in the soil nitrification pathway. The altered AOB community structure, in response to the nitrification inhibition by these rice varieties, can impact the soil's nitrogen transformation processes. This, in turn, can affect the nutrient availability for the plants and influence the overall productivity

and environmental sustainability of rice cultivation (Luo et al. 2019). High nitrogen availability observed may result from enhanced mineralization processes, reduced nitrification rates leading to lower nitrate production and subsequently diminished denitrification and leaching losses, and/or decreased plant nitrogen uptake due to suboptimal plant growth (Luo et al. 2019; Sugiyama and Yazaki 2014).

Soil physical and chemical changes caused by the change of irrigation mode reshaped rice rhizosphere microbial

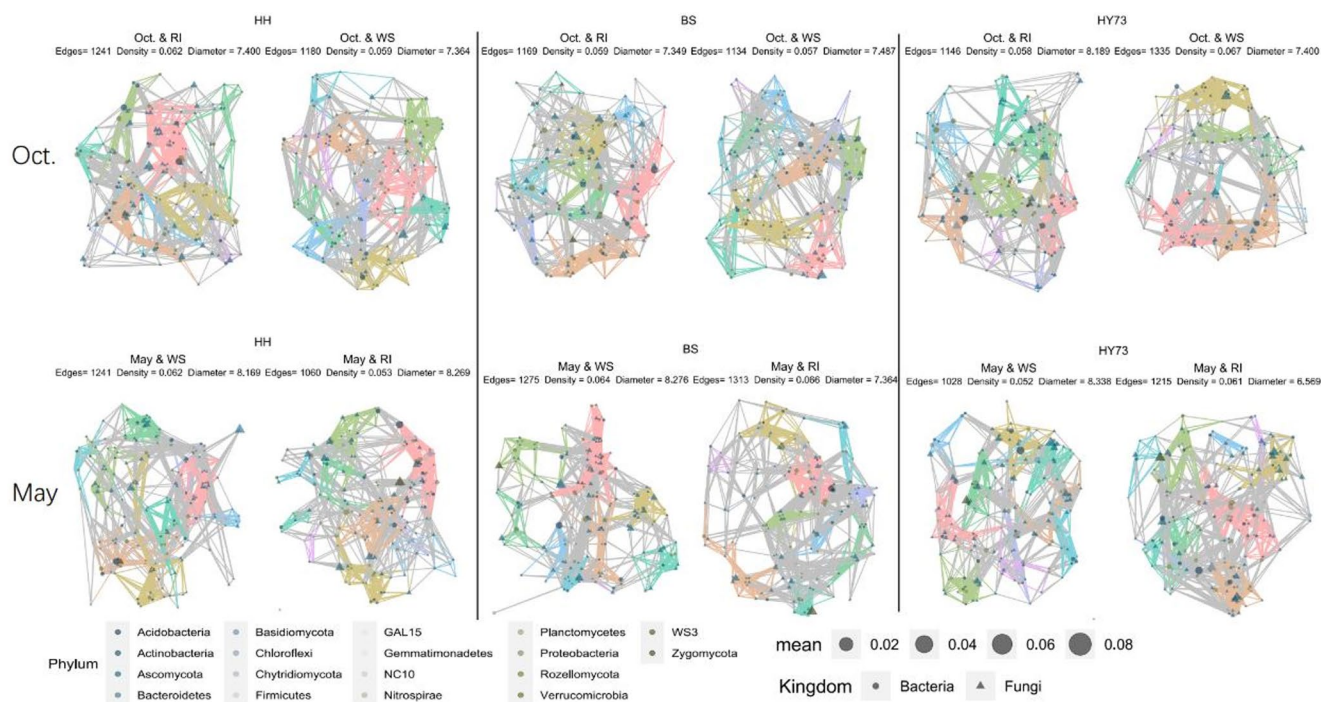


Fig. 9 Bacterial and fungal co-occurrence network among two irrigation methods and three rice varieties. Networks were constructed based on random matrix theory (RMT) algorithms. The connection stood for

a strong (Spearman's $\rho > 0.78$) and significant ($p < 0.001$) correlation. The nodes represented unique sequences in the data sets. The size of each node was proportional to the relative abundance

community, and microbial symbioses can mitigate drought stress in crops. The temporal variation of rhizosphere microbial community can largely attribute to the fluctuation of soil temperature between seasons, which can drive the distribution of soil microbial communities. In addition, the rhizosphere tends to select and recruit divergent microorganisms to stimulate rice growth among different stages (Juyal et al. 2019). Some studies indicated that the drought-mediated enrichment of Actinobacteria in root-associated microbiomes is a pattern broadly shared across a wide diversity of plants (Naylor et al. 2017; Santos-Medellín et al. 2021). The current research indicates that drought was the primary factor responsible for altering the composition of rhizosphere microbes. This alteration resulted in a reduction in microbial abundance and led to a more homogenized microbial community function. Previous research has shown that alterations to the microbiome caused by drought continue to be evident during the recovery phase (Santos-Medellín et al. 2021), which is consistent with this study. Additionally, certain genera within the Actinobacteria phylum are consistently enriched in response to drought conditions, including *Actinoplanes*, *Catellatospora*, *Dactylosporangium*, *Pseudonocardia* and *Amycolaptopsis*, which previously have been associated with plant-growth and grain yield promotion (Mohammadipanah et al. 2015).

The rhizosphere microbes play an important role in crop health and sustainable productivity (Ding et al. 2019;

Khalid et al. 2023a; ur Rahman et al. 2023). In our study, the enriched arbuscular mycorrhizal fungi (AMF) in HY73 fields may contribute to the high yield, as AMF are essential in N and P uptake. In addition, AMF have been reported to interact with mycorrhiza helper bacteria and endo-bacteria to promote rice grain yield (García-Orenes et al. 2016; Wang et al. 2022). The enriched *Nitrosomonas* and *Nitrospira* in HY73 soils may contribute to the nitrogen transformation processes. The tillering stage is crucial for rice yield when rice exhibits the most rapid growth and development (Abdou et al. 2021). The results show that bacteria with chemoheterotrophy, nitrification and aerobic nitrite oxidation functions in HY73 rhizosphere increased significantly in June and July. The bacteria corresponding to the above three functions are closely related to the fixation of N in the soil and the uptake of N by plants (Chen et al. 2022). NN showed a significant increase in the tillering stage, particularly in HY73. WS conditions increased the abundance of AOB, which directly affects soil nitrification, a critical step in the N cycle (Chunmei et al. 2020). HY73 may possess strong redox abilities, allowing it to efficiently assimilate and absorb nitrogen for biosynthesis, with high dehydrogenase and cytochrome oxidase activity (Cheng et al. 2022).

Low water irrigation significantly increases soil oxygen, EC, and pH, which helps mitigate the toxicity of reducing substances and heavy metal ions in the rhizosphere soil (Wang et al. 2023). The decrease in iron-respiring bacteria

contributes to the formation of iron plaque on the roots, affecting the chemical behavior and biological effectiveness of elements in the soil, such as As, Zn, and Fe, through adsorption and co-precipitation (Deng et al. 2010; Li et al. 2021). Although the abundance of iron-respiring bacteria decreases under 50% water irrigation, the increase in soil oxygen content may counteract their adverse effects. However, it is still unclear how the stress mitigation ability of HY73 in 50% water irrigation has changed, and further research is needed.

Microbial communities in rhizosphere soil are influenced by abiotic conditions and root-derived signals, such as root exudates, root overlap, and soil nutrients (Li et al. 2024; Ulbrich et al. 2022). In a previous study, root exudates have been demonstrated to selectively induce the growth of rhizosphere bacteria (Xiong et al. 2020). Recent work has indicated that the gram-positive bacteria including *Actinobacteria*, *Verticillium virens*, and *Sclerotinia* produce a variety of compounds such as polysaccharides and glycoside hydrolases (Chen et al. 2022). Furthermore, Santana et al. demonstrated that root exudates promoted the enrichment of *Bacillus sp.* ESA 402, one of PGPR in the rhizosphere of sorghum (*Sorghum bicolor*), promoting the growth of the sorghum under drought stress (Santana et al. 2020). While, AMF plays important roles in promoting plant resistance to biotic and abiotic stresses and AMF infection can significantly improve the expression of plant-related genes (Sui et al. 2019; Tian et al. 2020) and the ABA hormone level of wild rice through the root exudates, strigolactones and flavonoids (Sugiyama and Yazaki 2014). However, our study did not investigate root exudates or the rhizosphere microecology of WDR, which will be the focus of future research.

Conclusion

In conclusion, our study elucidates the intricate relationship between the rhizosphere microbial community of the drought-resistant rice variety HY73 and its ability to achieve high yields under 50% water irrigation. The enhanced nitrogen content, particularly due to the increased abundance of ammonia-oxidizing bacteria represents a potential mechanism contributing to the superior grain yield of HY73. These findings underscore the importance of microbial-mediated nitrogen metabolism in plant growth and drought resistant. Specifically, the higher grain yield in HY73 can be attributed to several interrelated factors: the proliferation of AOB during the tillering stage, which enhances nitrogen availability; the modulation of key enzymes that facilitate the conversion of sucrose to starch, optimizing energy storage for grain production; and the beneficial interactions with certain microbial phyla, such as Proteobacteria, Chloroflexi,

Gemmatimonadetes, and Ascomycota, which are positively associated with rice yield.

The perspectives of the current study highlighted the potential for manipulating the rhizosphere microbial community to enhance crop resilience and productivity. The identification of Myrothecium and other AMF as contributors to soil nutrient availability suggests that targeted inoculation strategies could be developed to further improve the performance of WDR varieties. This research may open avenues for investigating the long-term impact of water-saving irrigation on soil health and the sustainability of microbial communities.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11274-025-04677-0>.

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Author contributions Junguo Bi, Jiayi Li designed the experiments, obtained resources, and acquired funding. Saeed ur Rahman, Yuchong Long and Nan Hui conducted the experiments. Martin Romantschuk, Xianxian Zhang and Junqiang Zhang analyzed the data and Danping Hou, Jinsong Tan, Qingyu Bi, Hui Xia, Xinqiao Yu and Lijun Luo wrote the manuscript and took part in the writing process and edited the manuscript. Xinxin Liu supervised the study. All authors read and approved the final manuscript.

Data availability 16 S rRNA and ITS gene sequencing raw data that support the findings of this study are available in <https://www.ncbi.nlm.nih.gov/>. The first BioProject ID in Sequence Read Archive (SRA) of NCBI is PRJNA1027973. The submission name is: Water-saving and drought-resistant rice Raw sequence reads bacteria. The second BioProject ID in Sequence Read Archive (SRA) of NCBI is PRJNA1036150. The submission name is: Water-saving and drought-resistant rice Raw sequence reads fungi.

Declarations

Competing interests The authors declare no competing interests.

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