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Microbial Community Responses to Alternate Wetting and Drying in the System of Rice Intensification

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Continuous flooding in rice production presents significant challenges, such as increased labor intensity and soil degradation. However, when properly implemented, alternate wetting and drying can mitigate these issues. Despite its potential advantages, the effects of different water management practices on the soil microbiome are not well understood. This study explored how intermittent flooding and drying influence the soil microbiome by analyzing microbial communities under varying moisture conditions using Illumina sequencing. The results showed notable shifts in the abundance of Bacillota and Actinomycetota in response to fluctuations in water levels, although the overall microbial abundance returned to its original state under stable moisture conditions. In contrast, the abundance of Chloroflexota, which increased during waterlogging, remained elevated even under dry conditions. Additionally, microbial interactions were more pronounced during waterlogging compared to both moist and dry conditions. Overall, this research underscores the significant role of water management in shaping soil bacterial communities.

Keywords : alternate wetting and drying, microbiome, System of Rice Intensification, waterlogging

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Traditional rice cultivation often demands significant inputs, including fertilizers, water, and seeds, which can lead to diminishing returns for farmers. To address these inefficiencies, De Laulanie introduced the System of Rice Intensification (SRI), an innovative approach to rice farming that leverages the crop's natural physiological capabilities to achieve optimal yields using lesser external inputs (Berkhout et al., 2015; Uphoff, 2024). Unlike conventional methods, which involve closely spaced seedlings and continuous flooding from planting to harvest, SRI advocates for wide seedling spacing and water management that promotes moist, aerated soils interspersed with dry periods. The water management approach known as alternate wetting and drying (AWD) has demonstrated the ability to increase grain yields while providing an ecologically sustainable alternative by conserving water (Uphoff et al., 2002).

Waterlogging was reported to affect plant growth and development with some plants adopting by altering their physiological processes. It leads to reduced gas exchange between plant parts and their environment, limiting photosynthesis as well as stomatal closure due to impaired root signaling that lead to plant senescence and death (Else et al., 2009). However, rice exhibits a unique adaptation to waterlogging through the expression of alpha-amylase,

which converts starch into soluble sugars like sucrose under low oxygen conditions (Zhou et al., 2020). While other crops, such as cotton (Wang et al., 2017), wheat, barley (De San Celedonio et al., 2014), and maize (Huang et al., 2022), experience yield losses during critical growth stages under waterlogging, rice does not show significant yield loss under similar conditions. However, environmental degradation can result from waterlogging.

Continuous flooding in the traditional rice cultivation method effectively reduces diseases and insect pests but comes with several significant drawbacks. Waterlogging can neutralize soil pH, resulting in greenhouse gas emissions, organic matter decomposition, and reduced nutrient availability (Ding et al., 2021; Szejgis et al., 2024). Flooding can also lead to the leaching of excess nitrogen and nitrate (Shrestha et al., 2019) and increase soluble phosphorus concentrations, heightening the risk of phosphorus runoff into surface waters (Wang et al., 2022). Additionally, reduced soil oxygen impairs microbial activity by limiting electron acceptors, thereby affecting macro-nutrient availability (Balakhnina et al., 2012).

Microbial community stability is crucial for plant resilience to environmental stress. Flooding depletes soil oxygen and carbon, impacting microbial metabolism (Rupngam and Messiga, 2024). These transient changes can lead to the dominance of anaerobic microorganisms, such as fermenters, sulfate reducers, and methanogens (Barneze et al., 2023), which thrive by utilizing alternative electron acceptors like nitrate and sulfate (Rupngam and Messiga, 2024). Shifts in microbial diversity influence microbial activity, soil fertility, greenhouse gas emissions, and overall ecosystem functioning (Zhang et al., 2020). The effects of flooding are often temporary, with conditions reverting to their original state once aerobic environments are restored (Humphries et al., 2023). Alternating wet and dry cycles have been shown to improve soil quality and plant health by increasing micronutrient availability, enriching microbial diversity, and reducing the bioavailability of heavy metals in the soil (Majumdar et al., 2024). These benefits are attributed to enhanced aerobic conditions, which promote the activity of beneficial aerobic bacteria, ultimately supporting better yield development (Thakur et al., 2023).

Previous studies have explored microbiome dynamics under specific moisture conditions, such as flooding (Fang et al., 2024) and drying (Santos-Medellin et al., 2021). However, understanding microbiome dynamics across the diverse moisture regimes characteristic of SRI is crucial. These regimes include moist, waterlogged, and dry conditions, which create cyclic oxic and anoxic environments.

Such fluctuations promote the dominance of aerobic and anaerobic microbes at different stages. This study aims to examine microbial shifts driven by alternating waterlogging and drying in rice fields and assess the stability of the soil microbiome for subsequent cropping seasons.

In the present study, we collected samples from three rice fields in which rice was rotated with tomatoes for five years. The fields are in Buyeo (36.16016°N, 126.99054°E; 36.15841°N, 126.99462°E; 36.15649°N, 126.98135°E), Chuncheonbukdo province, Korea. The fields were subjected to varying water conditions: moderately moist soil with visible moisture but no stagnant water, henceforth referred to as moist soil; field with completely submerged soil (water level > 2 cm), henceforth referred to as waterlogged soil; field where there was no indication of soil surface water, henceforth referred to as dry soil. Five replicates from each field were analyzed. Each replicate was obtained from a quadrat at the four corners and the center of the field. The plants were uprooted, and the roots were agitated to remove loosely attached soil particles, retaining only the rhizosphere. The rhizosphere samples were subsequently placed in 50 ml tubes. To obtain the rhizosphere samples, 20 ml of sterile distilled water was added to the roots and agitated. The roots were then removed and discarded. The aliquot was centrifuged, and the resulting pellet was stored at –80°C prior to DNA isolation.

To confirm the observations from the field samples, different water conditions observed in the fields were replicated in the greenhouse using a common starting soil. Soil was collected from pepper field and utilized as the initial substrate for evaluating the effects of various water conditions on the microbial community. The pepper field soil was chosen to eliminate any potential influence from previous rice crops, ensuring a uniform microbial community at the outset for fair comparisons. Seeds of rice (Variety Sindongjin) were sown on seedling trays and subsequently transplanted to soil in a 1 m × 1 m metal pan at 20 cm intervals. The seedlings were maintained under moist conditions by applying water at 50% holding capacity for two weeks, after which five plants were sampled and the rhizosphere soil collected as described in the field sampling protocol. The plants were then maintained at full water capacity by continuously covering the soil with water for two weeks, followed by sampling and collection of rhizosphere soil from five plants. Subsequently, the plants were subjected to dry conditions by applying water at 25% capacity for two weeks, after which rhizosphere samples were collected from five plants.

The metagenomic DNA from the samples was isolated using Exgene Soil DNA (GeneAll, Seoul, Korea) accord-

ing to the manufacturer's instructions. After performing quality control, only qualified samples proceed to library construction. The library preparation and sequencing were performed by Macrogen (Seoul, Korea). The sequencing library was created by randomly fragmenting the DNA sample, followed by ligation of 5' and 3' adapters. The size distribution of the PCR-enriched fragments was verified using an Agilent Technologies 2100 Bioanalyzer with a DNA 1000 chip. Finally, the libraries were quantified using quantitative PCR (qPCR), following the Illumina qPCR quantification protocol (Illumina, San Diego, CA, USA). For cluster generation, the library was introduced into a flow cell, where fragments were captured on a surface coated with oligonucleotides complementary to the library adapters. Each fragment was then amplified into distinct, clonal clusters via bridge amplification. Upon completion of cluster generation, the templates were sequenced using Illumina's sequencing-by-synthesis technology.

Raw sequence data were prepared and analyzed utilizing QIIME 2 (Quantitative Insights into Microbial Ecology, version amplicon-2024.10). High-quality demultiplexed forward reads were trimmed at the 270th position on the right and the 20th position on the left, while the reverse reads were trimmed at the 200th and 22nd positions, based on sequence quality assessments. The quality reads were subsequently denoised using DADA2 to detect and correct Illumina amplicon sequence data including filtering, dereplication, identification of chimera, sample inference and merging the paired end sequences. The amplicon sequence variant (ASV) table was generated to record the abundance of each ASV per sample.

Taxonomic classification was done using a pre-trained Naive Bayes classifier trained on the Silva 138 database where sequences were trimmed to represent only the region between the 515F/806R primers. The classifier was used to assign taxonomic information to the ASV sequences using the sklearn module. A summary of the taxonomic annotations was then compiled and exported as a taxonomy table. ASVs not belonging to the bacterial kingdom such as chloroplast and mitochondria were filtered. The taxonomy and feature table were imported into R (R Software, R Foundation for Statistical Computing, Vienna, Austria) and utilized for further analysis and visualization.

Statistical analysis was conducted utilizing the Microeco package (Liu et al., 2011) in R software (v 4.3.1). The analysis of variance (ANOVA) test was used for differential abundance analysis at phylum and class level using the filter threshold of 0.001. The significant difference between treatments was determined using adjusted P-value. The compositional relative abundance was converted to per-

centages and presented in bar plots.

Alpha diversity calculation was performed to investigate richness and diversity using indices such as Shannon diversity index and Chao1 richness index. Statistical significance was determined using ANOVA test. Beta diversity was calculated using Bray-Curtis dissimilarities distance. Non-metric multidimensional scaling (NMDS) was performed employing the "vegan" package and was used to visualize the distribution of the samples. The significance of compositional difference between samples was measured using permutational multivariate analysis of variance. RandomForest modeling was implemented to identify the key bacterial taxa associated with each water level using the "RandomForest" package. The result of the RandomForest analysis was visualized as a variable importance plot. The "ggplot2" package was employed for the visualization of alpha and beta diversity and differential abundance analysis.

To identify the key taxa from each water level, bacterial ASVs were utilized for the construction of a co-occurrence network at the Class level. To emphasize the most significant interactions, only statistically significant ($P < 0.05$), strongly positive ($r > 0.7$), and strongly negative ($r < -0.7$) relationships were considered. Gephi version 0.10.1 was employed for visualization of the co-occurrence network. The functional profile of the microbial communities was predicted using the Functional Annotation of Prokaryotic Taxa (FAPROTAX) database. The metagenome data was cross-referenced with this database to predict their biogeochemical traits, based on published research findings.

During our field survey, we observed that the standard practice for rice cultivation at the surveyed locations involved transplanting rice and maintaining it under moist conditions, followed by periods of waterlogging and intermittent drying until harvest (Fig. 1A). To explore the differences in microbial community structure under different moisture conditions, we analyzed the relative abundance of bacteria in the rhizosphere soil at phylum and class levels.

The relative abundance of Bacillota and Thermodesulfobacteriota was notably low under moist conditions, while Pseudomonadota showed an increase (Fig. 1B). In contrast, during waterlogging conditions, Actinomycetota were enriched, whereas the abundance of Acidobacteriota was lower compared to both moist and dry conditions indicating the ability of Actinomycetota to survive the anaerobic conditions during waterlogging. The highest relative abundance of Bacillota was observed in dry conditions, while Actinomycetota was found at its lowest levels.

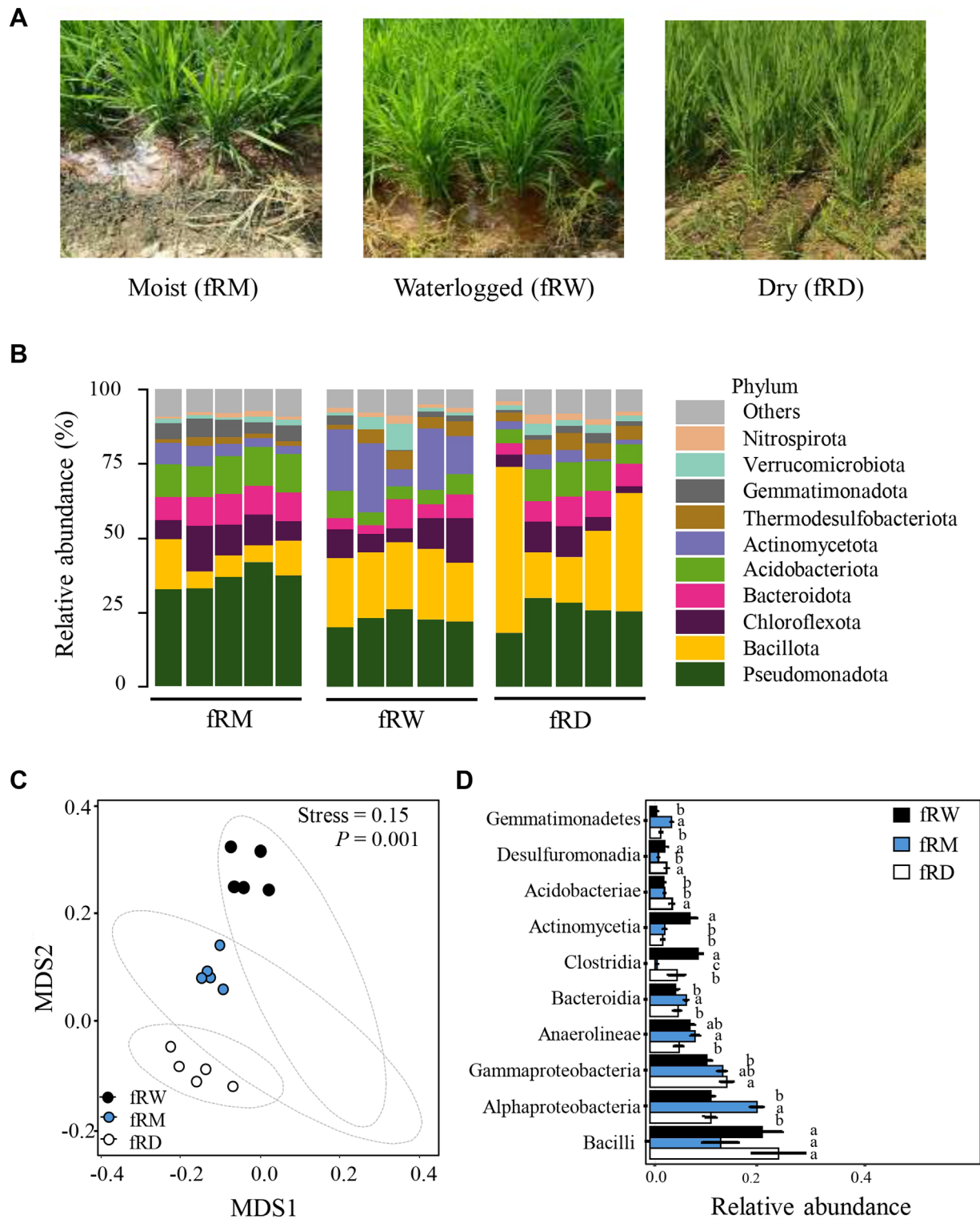The diversity of the bacterial community is an important

A

Moist (fRM)   Waterlogged (fRW)   Dry (fRD)

B

C

D

Fig. 1. (A) Description of cropping and watering sequence in the study area. (B) Relative abundance of bacteria at phylum level in the rhizosphere field samples. (C) Non-metric dimensional scaling (MDS) plot of the variation of bacterial community composition of rhizosphere from field samples. (D) Differential abundance of bacteria at class level in the rhizosphere field samples. Bars with the same letter are not significantly different at 0.05 probability using Duncan's new multiple range test. The error bars represent standard deviation.

index to explain the spatial distribution of bacterial taxa due to changes in moisture conditions. NMDS analysis of beta diversity revealed that the microbial communities in the field samples under different water regimes were distinctly different and clustered separately (Fig. 1C). Additionally, the diversity along both metric multidimensional scaling (MDS) 1 and MDS2 increase with increasing moisture level signifying the role of moisture in sustaining diverse
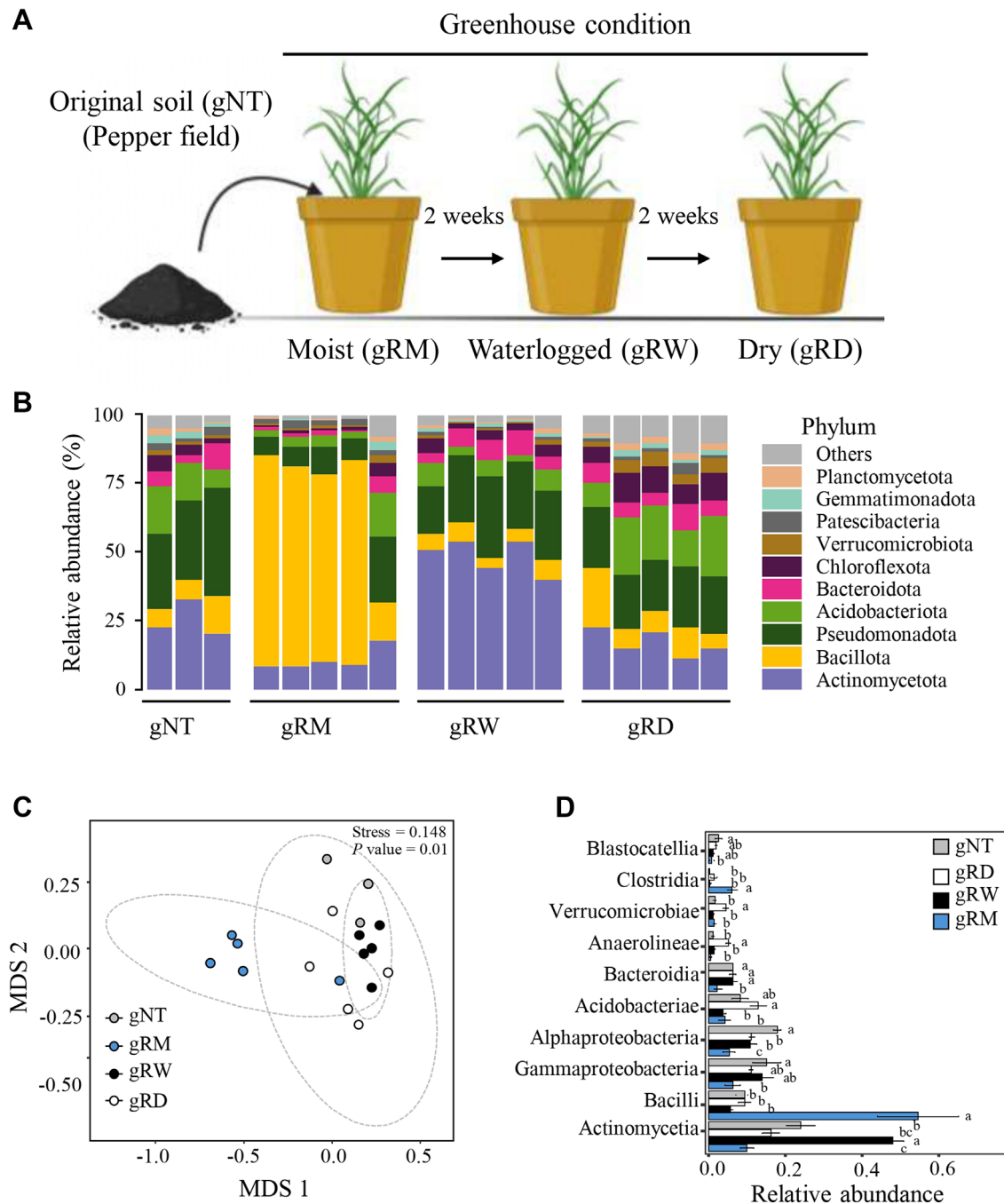

Fig. 2. (A) Arrangement of watering sequence experiment in the greenhouse. (B) Relative abundance of rhizosphere bacteria at phylum level affected by water conditions. (C) Non-metric dimensional scaling (MDS) plot of the variation of rhizosphere bacterial community composition from greenhouse samples. (D) Differential abundance of rhizosphere bacteria at class level influenced by water conditions in the greenhouse. Bars with the same letter are not significantly different at 0.05 probability using Duncan's new multiple range test. The error bars represent standard deviation.

groups of bacteria during rice cultivation.

The class level differential abundance was analyzed to better understand the diversity at finer taxonomic levels. The result of the field samples revealed a significant enrichment of Acidobacteriae in dry condition (Fig. 1D). At moist conditions, Alphaproteobacteria, Bacteroidia, and Gemmatimonadetes were significantly enriched while the waterlogging had enrichment of Clostridia, Actinomycetia,

and Desulfuromonadia.

The findings from the field study were derived from various locations, which may introduce limitations due to inherent soil differences. To validate these results, the field condition was replicated in a controlled greenhouse environment using a consistent starting soil (Fig. 2A). Our results indicated significant changes in the abundance of bacterial communities following water application during
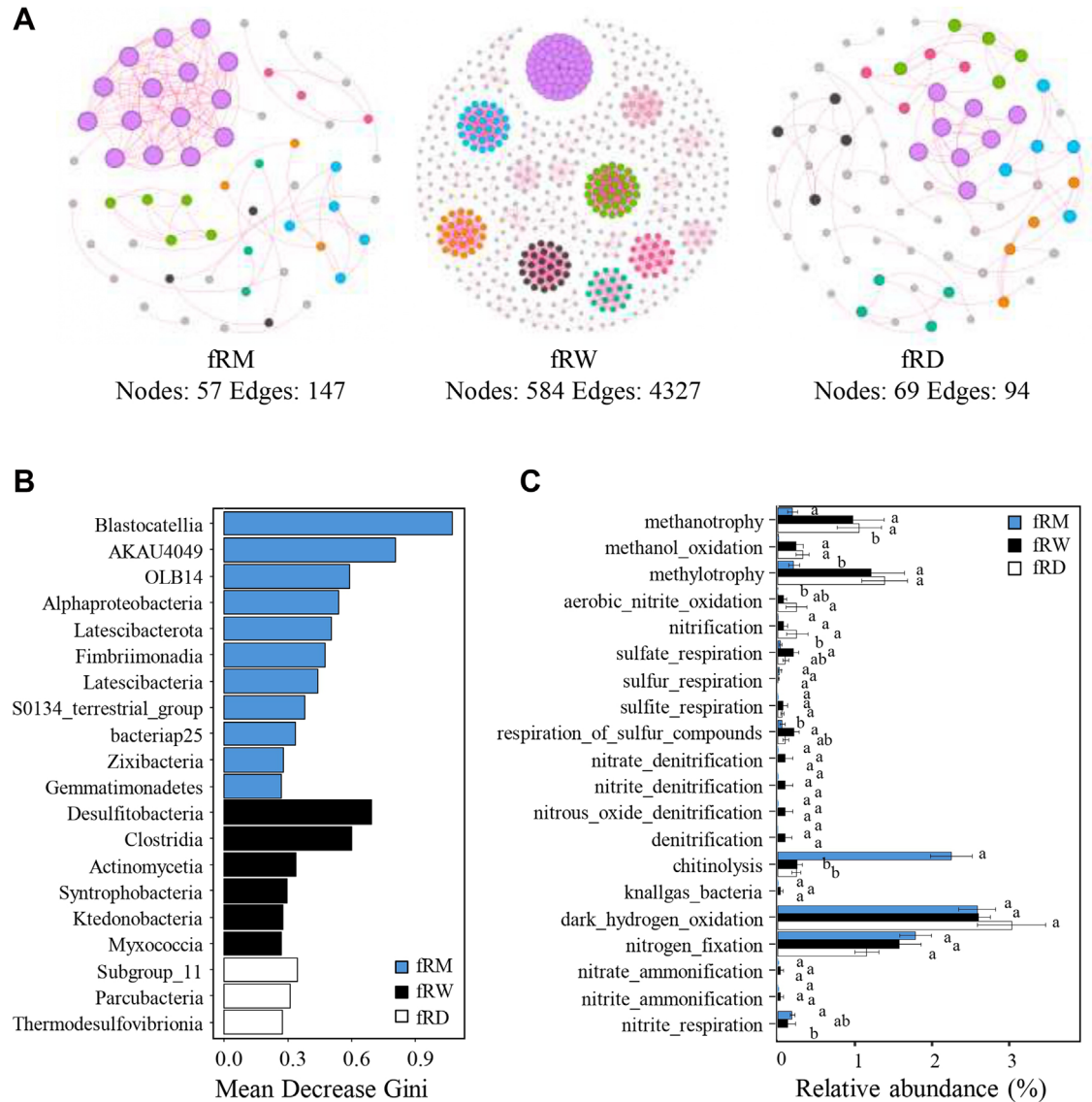

Fig. 3. (A) Co-occurrence network of bacteria from field soil under wet (fRM), waterlogged (fRW), and dry (fRD) conditions. Nodes color represents modules while positive and negative correlations are represented with red and green edges respectively. Node sizes are proportional to degree of interaction. (B) Variable Importance plot from the random forest classifier to identify the most important bacteria class in the rhizosphere of field rice under different water conditions. (C) The functions of the metagenome predicted using the functional annotation of prokaryotic taxa (FAPROTAX) database and differential abundance of the traits were calculated using ANOVA. Bars with the same letter within a group are not significantly different at 0.05 probability using Duncan's new multiple range test. The error bars represent standard deviation.

both the moist and waterlogged stages, with a stabilization of these communities observed at the dry condition. The major phyla detected significantly differ across the water levels, with specific taxa showing significant enrichment at each water level. In the original bulk soil, Pseudomonadota were the predominant bacterial group. However, when rice was cultivated and water was applied during moist and waterlogged conditions, the rhizosphere soil shifted to being dominated by Bacillota and Actinomycetota respectively (Fig. 2B). Following waterlogging, Pseudomonadota began to recover, followed closely by Actinomycetota, a trend reminiscent of the original field soil composition. While the abundance of Chloroflexota diminished during the moist condition, it became enriched in the dry condition.

The beta diversity of greenhouse samples also showed distinct clustering of microbial communities corresponding to different moisture levels, except for the dry condition, which did not form a distinct cluster (Fig. 2C). This confirms that each moisture level supports a unique microbial assemblage. The original soil samples displayed a more scattered distribution rather than clustering, suggesting greater variability in microbial composition compared to the more defined communities observed under controlled water levels.

The class level diversity from the greenhouse samples were consistent with those from the field, showing a significant reduction in Actinomycetia during moist condition, followed by a substantial enrichment under waterlogged condition (Fig. 2D). Conversely, Clostridia and Bacilli thrived during moist condition indicating their ability for growth under aerobic and anaerobic conditions. Under dry condition, there was an enrichment of Acidobacteriae, Anaerolineae, and Verrucomicrobiae.

Microbial network analysis was employed to assess the potential microbial interactions under different water levels in rice cultivation. In line with observed changes in beta diversity, water level induced changes in microbial networks that were more prominent in the waterlogged condition. Under moist condition, the distribution of nodes was sparse, encompassing only one major module with nodes that were strongly connected alongside five minor modules with lower degree of connectivity (Fig. 3A). Waterlogging induced a more complex network with a greater number of nodes which distinctly clustered into seven major modules. While connections between these major modules were limited, there were strong positive connections within modules. Under dry condition, the network had fewest edges with a single major module comprising of eight nodes. Despite the smaller number of nodes compared to waterlogged condition, inter-module connections were more

prominent under dry conditions.

RandomForest analysis was used to highlight specific bacterial groups as key distinguishing taxa at varying moisture conditions. For the bacterial community under moist conditions, Blastocatellia and Alphaproteobacteria emerged as the primary indicators (Fig. 3B). Under waterlogging, Desulfitobacteria, Clostridia, and Actinomycetia were the major distinguishing communities. In the dry condition, Parcubacteria and Thermodesulfovibrionia were identified as significant indicators.

The FAPROTAX analysis was performed to identify the changes in functions of the key microbiota in response to changing water levels. Chitinolysis and nitrite respiration were over-represented in the moist condition (Fig. 3C). Moreover, respiration of sulfur compounds and specifically sulfate were significantly over-expressed in the waterlogged condition. Functions related to denitrification including reduction of nitrate, nitrite, and nitrous oxide were more expressed under waterlogged conditions, although the differences were not statistically significant.

Our study revealed that Pseudomonadota, Chloroflexota, and Bacillota were consistently the most abundant bacteria associated with rice irrespective of water conditions. This observation aligns with the findings of Juliyanti et al. (2024), who reported that these phyla are predominant in both the rhizosphere and endosphere of rice plants. These microbial taxa were significantly influenced by fluctuations in soil moisture content. Fang et al. (2024) also observed the enrichment of Pseudomonadata in surface oxic soil conditions of rice and enrichment of Clostridia in anoxic conditions.

Notably, members of the phylum Bacillota and Actinomycetota exhibited the most pronounced response to changes in water conditions, with a substantial increase during waterlogging. This phenomenon can be attributed to the anoxic environment created when water saturates soil pores, favoring the proliferation of anaerobic microorganisms. Bacillota are known for their efficiency in fermentation processes. In oxygen-depleted environments, they employ nitrate ammonification and various fermentation pathways (Li et al., 2023). Corroborating this observation, Barneze et al. (2023) emphasized that anoxic conditions promote an increased presence of fermentative microorganisms in soil ecosystems. Zhang et al. (2019) also reported that Bacillota are sensitive to moisture stress. Interestingly, the abundance of Bacillota persisted even under drying conditions, likely due to its metabolic versatility, which enables survival in soils experiencing fluctuating oxic and anoxic conditions (Christensen and Rousk, 2024). This was confirmed by the predominance of Bacillota in the

isolated bacterial community. Despite significant shifts in abundance, diversity metrics remained relatively stable. This stability can be attributed to the reduction in aerobic bacterial populations during waterlogging, which facilitates the emergence of previously undetected anaerobic groups. These observations align with the findings of Humphries et al. (2023), who noted that microbiota often revert to their original state following short-term flooding events.

Microbial network analysis revealed increased positive interactions between microbial groups under wet and waterlogged conditions, suggesting that elevated moisture levels foster synergistic interactions within the anaerobic bacterial community. This phenomenon may be linked to the accumulation of metabolites produced by anaerobic bacteria, such as *Clostridium* sp. during fermentation processes (Guo et al., 2020), as well as the generation of biogas from anaerobic degradation by other groups, such as Anaerolineae and Desulfobacter (Harirchi et al., 2022).

This study identified members of the anaerobic class Clostridia and aerobic class Actinomycetia as key predictors of waterlogging. The presence of predominantly these groups from the rice rhizosphere further supports the hypothesis that beneficial bacteria can be active at both aerobic and anaerobic conditions contrary to the assumptions that waterlogging prevents the growth of beneficial plant microbiota. These classes of bacteria play an important role in plant protection evidenced by the overexpression of chitinolysis during waterlogging and plant growth promotion by enriching sulfur respiration which has the benefits of supplying sulfur to plants. Sulfur-reducing bacteria play a crucial role in agriculture by enhancing soil fertility through sulfur cycling and mineralization (Joshi et al., 2021; Ranadev et al., 2023). Additionally, they increase soil pH, which in turn improves the uptake of nitrogen and phosphorus making them ideal as bioinoculants (Joshi et al., 2021).

This study demonstrates that alternating waterlogging with drying in rice cultivation sustains the population of key plant growth-promoting bacteria. Recent literatures have demonstrated the agronomic benefits of AWD practices including increased grain yield, biomass production, and water use efficiency (Johnson et al., 2024; Wang et al., 2024). Our research has shown that AWD can enrich soil with beneficial bacteria, offering a sustainable approach to improving rice yield. We recommend incorporating multiple cycles of waterlogging during AWD under the SRI framework to enhance the abundance of Actinomycetota, a bacterial phylum previously identified as beneficial for plant growth. Furthermore, SRI has been shown to complement other sustainable cultivation practices, such as con-

servation agriculture (Carnevale Zampaolo et al., 2023). Future research should investigate the combined effects of these systems on soil microbiota to deepen our understanding of their ecological implications before widespread adoption by rice farmers.

Conflicts of Interest

No potential conflict of interest relevant to this article was reported.

Acknowledgments

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