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Root-Induced Changes in Soil Biological Activity under Different Rice Cultivation Systems

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Abstract Rice cultivation systems play a critical role in shaping rhizosphere processes and regulating soil biological activity through root-mediated interactions. Different cultivation practices, including conventional flooding, alternate wetting and drying, intermittent irrigation, and organic management, can significantly alter root morphology, exudation patterns, soil physicochemical properties, and microbial habitats. This review synthesizes current knowledge on root-induced changes in soil biological activity under diverse rice cultivation systems, with a particular focus on rhizosphere microbial communities, soil enzyme activities, nutrient cycling processes, and their implications for rice productivity. Root exudates and oxygen release from rice roots serve as key drivers of microbial diversity and functional activity, influencing carbon, nitrogen, and phosphorus transformations in the rhizosphere. Water-saving cultivation systems often enhance microbial functional diversity and nutrient-use efficiency by creating dynamic aerobic-anaerobic conditions, whereas organic cultivation promotes beneficial microorganisms and improves soil ecological resilience. Furthermore, root-induced biological processes contribute to enhanced nutrient acquisition, stress tolerance, soil health, and sustainable yield formation. The review also highlights recent advances in multi-omics approaches for elucidating root-soil-microbe interactions and discusses future research directions aimed at developing environmentally sustainable and resource-efficient rice production systems. Understanding the mechanisms underlying root-induced soil biological activity will provide valuable insights for optimizing rice cultivation practices and improving agroecosystem sustainability.

Keywords Rice cultivation systems; Rhizosphere biological activity; Root exudates; Soil microbial communities; Nutrient cycling

1 Introduction

Rice is a cornerstone of global food security but is also one of the largest consumers of freshwater and a major source of greenhouse gas emissions (Nawaz et al., 2022). Traditional continuously flooded systems dominate world rice area, yet their long-term sustainability is threatened by water scarcity, climate variability, energy costs, micronutrient imbalances, and environmental externalities such as methane emissions and arsenic accumulation (Bwire et al., 2024). In response, water-saving cultivation methods such as aerobic rice, alternate wetting and drying (AWD), direct seeding, and the System of Rice Intensification (SRI) are being promoted to reduce water inputs and environmental impacts while maintaining yields. These systems shift soil conditions from persistently anaerobic to partly or largely aerobic, fundamentally altering hydrology, redox status, and nutrient dynamics in paddy soils. Understanding how such shifts affect belowground biological processes is central to designing resilient rice-based agroecosystems.

The evolution of rice cultivation systems from conventional flooded paddies toward aerobic and intermittently flooded systems is driven primarily by shrinking water resources and climate pressures (Midya, 2025). Flooded rice can require 900-2250 mm of water per season, whereas aerobic rice and AWD can reduce total water input by 25%-70%, increase water productivity by 64%-80%, and substantially lower methane emissions, often with limited penalties in yield when properly managed. However, these shifts come with trade-offs, including micronutrient disorders, increased weed pressure, possible yield penalties in sub-optimal environments, and altered emission profiles of other greenhouse gases. Systems such as SRI and AWD are highlighted as climate-smart options that can simultaneously improve water use efficiency, sustain or enhance yields, and reduce methane emissions, thereby contributing to both food security and climate mitigation agendas. As adoption expands, questions arise about their long-term effects on soil health, particularly the biological component underpinning nutrient cycling and soil fertility (Midya et al., 2021).

Plant roots are primary drivers of soil biological activity, creating rhizosphere “hotspots” where microbial biomass, extracellular enzyme activities, and nutrient turnover are strongly stimulated by rhizodeposition and root-induced changes in moisture and pH. Root exudates—comprising sugars, organic acids, amino acids, and secondary metabolites—act as biochemical signals and energy sources that shape rhizosphere microbial communities, regulate enzyme kinetics, and modulate carbon and nutrient cycling, including rhizosphere priming effects and mobilization of mineral-protected organic matter (Yusuf et al., 2025). Studies across crops show that root traits (including architecture, biomass, and nutrient status) tightly couple with microbial biomass, hydrolase activities, and nitrogen acquisition, with high root N content and larger root systems generally associated with stronger stimulation of microbial enzyme activity and nutrient cycling in the rhizosphere. In rice, the rhizosphere microbiome and exudate profiles respond sensitively to environmental stresses such as drought and to genotype, with shifts in bacterial community composition (e.g., enrichment of Actinobacteria, Bacillus) closely linked to changes in organic acids, amino acids, and phytohormones in exudates, and feeding back to plant stress adaptation and nutrient acquisition. Water management and cultivation method in rice (flooded, AWD, aerobic, SRI) create contrasting redox and moisture regimes that are known to alter microbial community dynamics and soil chemical quality, yet the specific root-induced changes in microbial biomass, enzyme activities, and rhizosphere processes under these systems remain poorly quantified.

Investigating root-soil-microbe interactions across different rice cultivation systems is therefore critical for reconciling water-saving, yield stability, and soil health goals. Shifts from continuously anaerobic to intermittently or fully aerobic soils are expected to restructure microbial communities, change the balance of carbon- and nutrient-acquiring enzymes, and modify rhizosphere priming, with implications for organic matter turnover, nitrogen use efficiency, and greenhouse gas balances. Evidence from rice and other crops indicates that root system architecture and exudate chemistry can redistribute microbial activity with depth, create distinct enzyme activity hotspots, and govern microbial nutrient limitation patterns, suggesting that management-induced changes in rooting and water regimes may be leveraged to enhance nutrient cycling efficiency and resilience (Lattacher et al., 2025). In rice fields, where new cultivation systems such as aerobic rice, AWD, and SRI are being promoted at scale to address water scarcity and climate impacts (Soltani et al., 2024), there is a clear need to elucidate how roots under these contrasting hydrological and management regimes induce changes in soil biological activity. Such knowledge will support the design of rice cultivation strategies that not only save water and reduce emissions, but also build functionally robust rhizosphere communities, sustain soil fertility, and secure rice production under increasing environmental stress.

2 Rice Cultivation Systems and Rhizosphere Environmental Characteristics

2.1 Soil ecological characteristics of conventional flooded rice cultivation

Continuous flooding creates a vertically stratified soil system with oxic surface layers, an oxic-anoxic rhizosphere, and a largely anoxic bulk soil. Oxygen is rapidly depleted after flooding, and anaerobic microorganisms such as fermenters and methanogens dominate the bulk soil, making methane the final product of organic matter degradation. In contrast, oxygen released from rice roots forms microscale oxic zones around roots that host aerobic processes and steep redox gradients (Liesack et al., 2000; Ding et al., 2019).

These oxic-anoxic interfaces structure rhizosphere communities and depth profiles of functional groups. Methanotrophs peak near the oxic-anoxic boundary, while methanogens and total organic carbon are highest in deeper rhizosphere layers, indicating methane production from plant-derived carbon and aerobic consumption near the root zone (Lee et al., 2015). Bacterial and archaeal communities differ clearly between oxic, oxic-anoxic, and anoxic zones, with higher microbial abundances and stronger network interconnections in rhizosphere soil than in pore water (Zecchin et al., 2023).

2.2 Rhizosphere environmental changes under water-saving cultivation systems

Under alternate wetting and drying (AWD) or related moderate drying regimes, soil redox conditions and solution chemistry fluctuate with irrigation cycles. Alternate moderate wetting and drying at grain filling decreases soil pH and increases redox potential and electrical conductivity compared with continuous irrigation, with these variables rapidly recovering after re-watering (Li et al., 2018). AWD also increases root-zone macroporosity and pore connectivity relative to continuous flooding, enhancing water sorptivity without increasing mechanical hardness (Islam et al., 2024).

These physical and chemical shifts feed back on root function and rhizosphere biological processes. AWD combined with lower nitrogen rates maintains or improves root length, dry weight, and oxidation activity, while increasing soil oxygen, urease activity, and abundances of ammonia-oxidizing archaea and bacteria relative to continuous flooding (Figure 1). Controlled aerobic irrigation (e.g., drip) further reshapes rhizosphere microbiomes by favoring nitrifying-denitrifying taxa and strongly reducing methanogens, driven by higher oxygen availability and redox potential (Lau et al., 2025).

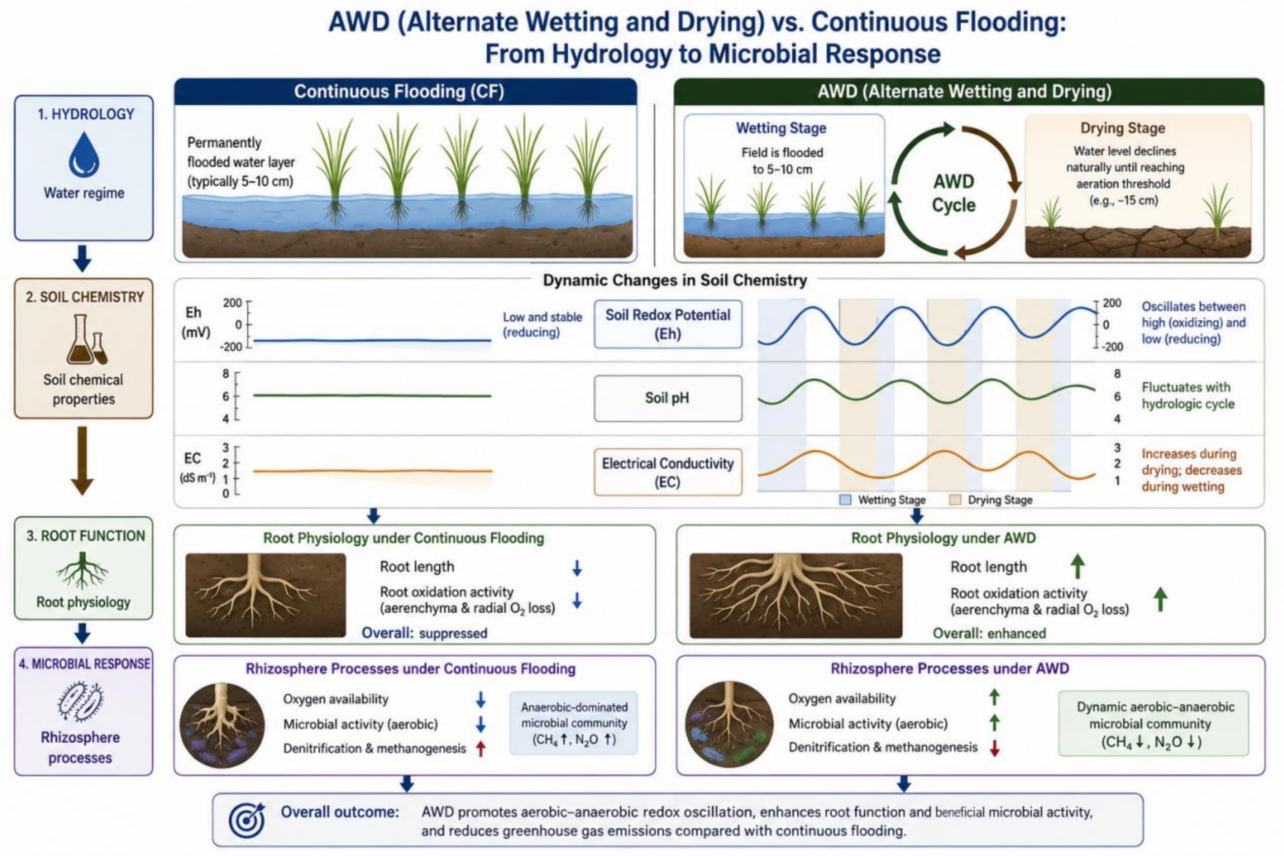

Figure 1 Conceptual framework illustrating how alternate wetting and drying (AWD) regulates soil redox dynamics, soil chemical properties, and downstream root and rhizosphere biological processes compared with continuous flooding irrigation

2.3 Effects of organic and ecological cultivation systems on the rhizosphere environment

Organic and ecological systems modify rhizosphere conditions mainly through enhanced organic inputs and reduced synthetic fertilizers. Rice-frog and rice-frog-organic systems increase soil protease and nitrate reductase activities and enrich denitrifying bacteria, while reducing urease activity and nitrifier abundance, indicating a shift in nitrogen transformation pathways (Yi et al., 2018). These systems also raise bacterial richness and diversity and link N-cycling communities positively to total carbon, total nitrogen, and C:N ratio, reflecting a more carbon-rich, biologically active rhizosphere (Yi et al., 2019).

Short- and long-term organic amendments further reshape rhizosphere structure and function. Rice straw inputs increase sucrase, cellulase, protease, organic carbon, and available nutrients, and enhance bacterial groups associated with nutrient transformation, whereas biochar tends to elevate microbial biomass, urease activity, pH, and available nitrogen and potassium. Bio-organic fertilizers and reclaimed-soil amendments can increase microbial diversity, adjust pH, and enrich beneficial bacterial taxa, supporting soil restoration and sustainable rice productivity (Liu et al., 2025; Qiao et al., 2025).

3 Root-Induced Processes Shaping Soil Biological Activity

3.1 Root morphological architecture and spatial distribution patterns

Rice has a hierarchically organized root system composed of primary, crown and lateral roots, whose spatial arrangement determines soil exploration and the location of rhizosphere “hotspots.” Deep and vertically extensive architectures favor capture of mobile resources such as water and nitrate, whereas dense topsoil foraging supports acquisition of immobile nutrients like phosphorus and potassium (Galindo-Castañeda et al., 2023). Differences in root growth angle, branching and depth therefore alter where carbon inputs and exudates enter the soil profile and where microbial communities are concentrated in flooded and water-saving systems (De Bauw et al., 2020).

Quantitative studies show that cultivars differ strongly in root length density, surface area and biomass distribution, with consequences for rhizosphere processes. Allelopathic rice tends to develop finer roots but higher root length and surface area densities, especially in the upper 0-5 cm and at lateral distances of 6-12 cm, which enhances soil contact and the delivery of allelochemicals to surrounding weeds. Three-dimensional functional-structural models of upland and wetland rice roots confirm that variation in lateral root types and biomass depth distribution strongly controls water and phosphorus uptake under contrasting moisture regimes (De Bauw et al., 2020).

3.2 Composition and dynamic changes of root exudates

Rice root exudates contain diverse low-molecular-weight compounds, including organic acids, amino acids, sugars and secondary metabolites, which act as major carbon and energy sources for rhizosphere microbes. Short-term ^{13}C-CO_2 pulse labeling shows that exudate-derived carbon is assimilated by microorganisms within hours, with fungi often outcompeting bacteria under flooded, low-redox conditions, and incorporation rates increasing as plants mature (Yuan et al., 2016).

Exudate composition is highly plastic and responds to genotype and environmental stress. Under drought, rice genotypes show altered profiles of phytohormones and metabolites in exudates, with increased abscisic acid, broad shifts toward higher organic acid release, and reduced amino acid exudation, changes that are tightly correlated with restructuring of rhizosphere bacterial communities (Li et al., 2023). In allelopathic cultivars, benzoic-acid derivatives accumulate in specific lateral soil zones and are linked to spatial patterns of weed suppression, indicating strong coupling between root distribution, exudate chemistry and ecological function.

3.3 Root oxygen release and nutrient transformation processes

Radial oxygen loss (ROL) from aerenchymatous rice roots creates oxic microsites around roots embedded in otherwise anoxic paddy soil, establishing sharp redox gradients that shape biogeochemical cycling. Genotypic differences in root porosity, diameter and adventitious root number translate into contrasting ROL capacities, with more porous, thicker roots and larger root systems generating higher internal and surface O_2 concentrations and deeper oxygen penetration into the surrounding soil (Li and Wang, 2013). These oxygenated zones enhance nitrification activity and nitrate accumulation in the rhizosphere, thereby improving nitrogen nutrition and growth of high-ROL cultivars compared with low-ROL types (Li and Wang, 2012).

ROL also drives iron redox transformations and coupled phosphorus dynamics at fine spatial scales. Imaging of O_2 and solute fluxes shows opposing oxygen and Fe(II) gradients extending 10-25 mm from root surfaces, where oxidative conditions promote formation of Fe(III) plaques that host redox-active metastable iron phases. Diel ROL rhythms induce repeated reduction-oxidation cycles in these plaques, mobilizing phosphorus from otherwise inert Fe (oxyhydr) oxides and substantially increasing P availability for uptake in rice paddies and other flooded systems (Li et al., 2025).

4 Changes in Soil Microbial Community Structure under Different Cultivation Systems

4.1 Responses of rhizosphere bacterial community composition and diversity

Rice roots consistently select distinct bacterial assemblages in the rhizosphere compared with bulk soil, often with lower richness but greater specialization and stability near roots (Tian et al., 2021). Across rice-growing regions, rhizosphere communities exhibit wider phylogenetic breadth and lower functional redundancy than bulk soil, indicating stronger functional differentiation driven by root inputs and nutrient hotspots. Genotype effects are detectable but modest: wild and domesticated Oryza lines host compositionally separable rhizosphere communities, suggesting that domestication altered root traits and associated bacterial recruitment (Shenton et al., 2016).

Environmental conditions and management further modulate these root-driven patterns. In saline-alkaline soils, different rice varieties assemble distinct rhizosphere microbiomes whose structure tracks both salinity level and genotype, with consequences for yield and grain quality (Zhong et al., 2025). Long-term straw and biochar amendments increase bacterial diversity and shift phylum-level composition, enhancing groups such as Chloroflexi and Actinobacteria in the rhizosphere and altering dominant families involved in carbon and sulfur transformations (Tang et al., 2021).

4.2 Fungal community succession and functional differentiation

Fungal communities at the soil-root interface show strong spatial and temporal structuring linked to plant traits and development. At the tillering stage, rhizosphere mycobiota are richer, more diverse, and more connected than endophytic communities, with dispersal limitation playing a larger role in rhizosphere assembly. These diverse assemblages correlate closely with functional traits such as root-shoot biomass ratios and N accumulation, suggesting that root growth strategies co-vary with fungal community structure and potential function (Guo et al., 2024).

Over the rice life cycle, rhizosphere fungal composition and assembly processes shift with growth stage and N fertilization. Beneficial Glomeromycota peak at heading, coinciding with elevated soil nutrients and N-acquisition enzyme activities, indicating targeted recruitment under high N demand. Saprotrophs increase as plant residues accumulate, while pathotroph abundance is highest at the seedling stage and declines as plant resistance strengthens, reflecting functional succession from defense-dominated to decomposition-dominated communities (Dong et al., 2023).

4.3 Enrichment of functional microbial groups and their ecological roles

Roots and cultivation systems jointly enrich key functional guilds involved in nutrient cycling and greenhouse-gas regulation. Across rice genotypes with contrasting N-use efficiency, rhizospheres accumulate bacteria linked to N transformations, Fe reduction, and sulfur metabolism, particularly within Proteobacteria and Chloroflexi (Chen et al., 2021). Higher yields are associated with greater abundance of functional bacteria, whereas stronger denitrifier gene abundance and activity correspond to lower N-use efficiency due to enhanced gaseous N losses.

Other functional groups respond to root-driven redox gradients and exudate regimes. In flooded paddies, methanotrophs, nitrifiers, and Fe-cycling bacteria can be selectively enriched and embedded in co-occurrence networks that both recruit beneficial taxa and exclude potential pathogens, thereby supporting community stability and ecosystem function (Li et al., 2025). Across paddies, aerobic methanotrophs metabolically couple methane oxidation to denitrification by releasing organic intermediates that fuel denitrifiers, linking carbon and nitrogen fluxes in hypoxic rhizospheres (Chen et al., 2024).

5 Soil Enzyme Activities and Biochemical Processes under Different Cultivation Systems

5.1 Variation in carbon-cycling enzyme activities

Carbon-cycling enzymes in rice systems, such as β-glucosidase, cellulase and related hydrolases, are consistently higher in rhizosphere than bulk soil, reflecting strong stimulation by root exudation and residue inputs (Jat et al., 2021). In cereal-based systems, rice-based climate-smart agriculture (CSA) increased rhizosphere β-glucosidase compared with maize-based CSA, and activities varied strongly with crop growth stage, indicating tight coupling to root development and carbon supply.

Management that enhances soil organic carbon (SOC) generally increases C-cycle enzyme activities. In saline-alkali rice fields, β-glucosidase and amylase activities declined with rising salinity, but remained positively correlated with SOC, showing that root-microbe interactions can promote C sequestration where salinity is moderate (Qu et al., 2021). Long-term tillage with residue return similarly increased rhizosphere cellobiohydrolase and β-glucosidase, with redundancy analysis linking these enzymes to SOC and labile C fractions, underscoring the role of root-driven C inputs in sustaining enzyme-mediated decomposition (Figure 2) (Wang et al., 2025).

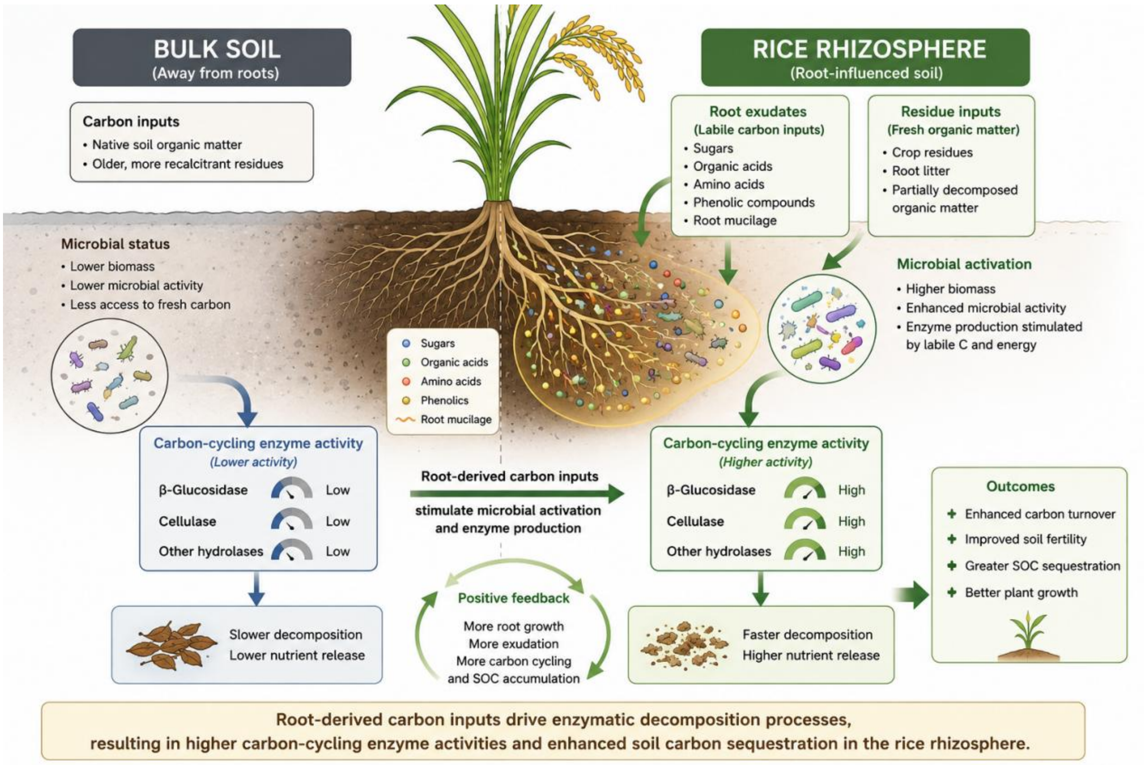

Figure 2 Conceptual comparison of carbon-cycling enzyme activities between rice rhizosphere and bulk soil, highlighting stimulation by root exudates and residue-derived carbon inputs

5.2 Response characteristics of nitrogen-cycling enzymes

Nitrogen-cycling enzymes in rice rhizosphere, particularly urease and protease, show strong sensitivity to cultivation pattern and N input. In rice-frog and organic systems, urease activity was lower than in conventional rice, where heavy urea use stimulated urease, while protease and nitrate reductase were enhanced under eco-agricultural management, indicating a shift toward microbially mediated organic N turnover and denitrification (Yi et al., 2018). Over centuries of rice cultivation, urease and protease rose sharply within the first 100 years and then declined, with amino-acid N closely related to these enzymes, suggesting that long-term root inputs and management co-regulate organic N pools and enzyme activities (Pan et al., 2022).

Water and aeration regimes further modulate N-cycling enzymes. Under alternate wetting and drying, urease, protease and ammonia oxidase activities in rice rhizosphere exceeded those under continuous flooding, while nitrate and nitrite reductase activities declined, paralleling increases in amoA and nifH genes and decreases in nirS and nirK (Xu et al., 2022). A global meta-analysis also showed that N addition generally increased urease in both rhizosphere and bulk soil, but rhizosphere C- and P-acquisition enzymes were less N-sensitive, highlighting distinct root-zone regulation of N-cycling relative to other nutrient-acquiring enzymes (Chen et al., 2023).

5.3 Phosphorus-transforming enzymes and changes in nutrient availability

Phosphorus-transforming enzymes, especially acid and alkaline phosphatases, form spatially complex hotspots around rice roots that respond dynamically to P availability. High-resolution imaging around flooded rice revealed strong P depletion zones near roots that coincided with phosphatase activity hotspots, confirming that local P shortage stimulates enzyme-driven mineralization in both rhizosphere and detritusphere (Fang et al., 2021). Across cereal systems, acid phosphatase tended to be higher in rhizosphere, whereas alkaline phosphatase could be greater in bulk soil where decomposing residues dominate, illustrating differing root and residue control on P-cycling enzymes (Jat et al., 2021).

Management practices alter phosphatase activity and thus P availability in the rice rhizosphere. Long-term biochar addition decreased labile P and Fe in flooded rice soils but triggered a compensatory increase in rhizosphere phosphatase, interpreted as an adaptive response to reduced P supply (Chen et al., 2022). In water-saving irrigated paddies with biochar, alkaline phosphomonoesterase activity rose by roughly 30%-45% and enzyme-extractable P declined, indicating enhanced microbial organic P mineralization under drier, more oxic root-zone conditions (Qi et al., 2024). Meta-analytic evidence from agricultural systems supports this pattern, showing that monoesterase activity is suppressed by inorganic P but strongly stimulated when organic P is abundant, emphasizing that root-induced P demand and organic P pools jointly control phosphatase expression and P mobilization.

6 Root-Induced Regulation of Soil Nutrient Cycling and Ecological Functions

6.1 Effects of rhizosphere carbon inputs on microbial metabolism

Rice roots continually allocate assimilated carbon to the rhizosphere as exudates and other rhizodeposits, providing highly available substrates that rapidly enter microbial biomass and drive C cycling. Short-term ^13 CO_2 labeling demonstrates that exudate-derived C is assimilated into phospholipid fatty acids of diverse microbial groups within 6 h, with incorporation rates increasing as rice plants mature, showing a strong growth-stage control of microbial C use (Yuan et al., 2016). Nitrogen fertilization further enhances this flux of rhizosphere C: added N stimulates plant biomass and root exudation, leading to higher ^13C incorporation into microbial biomass in both rhizosphere and bulk soil and intensifying rhizosphere influences on surrounding microorganisms (Liu et al., 2019).

The balance between microbial anabolism and catabolism in this C-rich zone is sensitive to management and root-driven changes in substrate stoichiometry. Long-term addition of rice straw or manure lowers microbial carbon use efficiency in rhizosphere soil compared to mineral fertilization alone, because greater exudation and nutrient uptake by plants increase the local C:N ratio and favor respiratory C losses (Chen et al., 2020). Despite this reduced efficiency, organic inputs promote higher microbial growth rates and necromass accumulation, strengthening soil organic C pools, so root-derived C inputs ultimately increase both microbial respiration and long-term C sequestration in paddy soils.

6.2 Root-driven nitrogen transformation and improvement of nitrogen use efficiency

Root traits and management jointly regulate nitrogen transformation pathways around rice roots, with consequences for nitrogen use efficiency (NUE) and gaseous losses. Integrative cultivation practices that combine optimized N supply, increased planting density, alternate wetting and drying, and organic fertilizers enhance root length, dry weight, and oxidation activity, while also increasing total organic acids in root exudates (Gu et al., 2023). These root improvements are accompanied by elevated rhizosphere urease and invertase activities and greater bacterial diversity, alongside higher nitrate and lower ammonium concentrations, indicating intensified ammonification and nitrification linked to better NUE.

Targeted N management can further coordinate root activity with rhizosphere microbial guilds to enhance NUE and reduce emissions. Mixed application of polymer-coated and rapid-release urea increases root oxidation activity and H^+ -ATPase activity, expanding oxygenated microsites and organic acid supply that favor Nitrospira and other nitrifiers, which correlate positively with nitrate content and N accumulation at booting (Zhu et al., 2024). At the same time, nano-enabled enhancement of photosynthesis boosts carbohydrate transfer belowground, stimulates ammonification and nitrification, and suppresses denitrification, improving NUE and lowering N_2O and NH_3 emissions without sacrificing yield (Wang et al., 2025).

6.3 Rhizosphere phosphorus mobilization and cycling mechanisms of other mineral nutrients

Rice roots mobilize sparingly available phosphorus through tightly coupled redox and biochemical processes in their immediate vicinity. High-resolution imaging shows that radial oxygen loss from roots generates localized redox hotspots where available P, oxygen, and acid phosphatase activity co-occur within a few millimeters of root surfaces, and P fluxes of about 10 pg cm^{-2} s^{-1} can be visualized near actively respiring roots (Li et al., 2023). Beyond rice, diel ROL rhythms in flooded systems produce redox-active iron plaques that repeatedly dissolve and reform, releasing P from otherwise inert Fe (oxyhydr)oxides into porewater and accounting for a substantial share of plant-available P at the global scale (Li et al., 2025).

In P-deficient rice rhizospheres, root-induced shifts in microbial assembly further enhance P mobilization and reveal a key role of fungi. Under low P supply, both bacterial and fungal communities change composition, but P-mobilizing taxa, especially fungal groups, become disproportionately enriched, and culture tests confirm higher phosphate-solubilizing capacity under deficiency than under adequate P (Sun et al., 2022). Parallel work in wetland sediments shows that root-mediated acidification, increased phosphatase activity, and enrichment of P-solubilizing and mineralizing genes together remobilize significant fractions of inorganic and organic P, although this resupply only partially offsets P depletion by uptake and mineral sequestration (Li et al., 2024).

7 Impacts of Root-Induced Soil Biological Activity on Rice Growth and Productivity

7.1 Relationships between rhizosphere biological activity and plant nutrient uptake

Root-microbe interactions in the rhizosphere strongly influence nutrient acquisition by regulating nutrient cycling genes and enzymes. In ratoon rice, a high-yielding variety had higher activities of C- and P-acquiring enzymes and greater abundances of carbon fixation, degradation, and P-cycling genes, which were tightly associated with higher available P, extractable and dissolved organic C, and ultimately higher ratoon yield (Wang et al., 2025). These functional traits alleviated C and P limitation in the rhizosphere and maintained nutrient supply during regrowth, directly linking microbial activity to nutrient uptake efficiency.

Specific functional consortia further enhance nutrient mobilization. A synthetic bacterial community isolated from rice/soybean intercropping increased rice biomass and P uptake via multiple pathways, including activation of soil available P and stimulation of root surface area and tip number, combined with up-regulation of Pi transporter genes in roots (Huimin et al., 2024). Inoculation with nitrogen-fixing Herbaspirillum R3 raised rhizosphere nitrate, ammonium, and available P and upregulated root N transporter genes, while enriching key nifH-harboring genera and increasing their diversity and stability, thereby strengthening N fixation capacity and nutrient uptake (Li et al., 2024).

7.2 Microbe-mediated mechanisms enhancing stress resistance

Rice can cope with saline-alkali stress by selectively recruiting keystone microorganisms with relevant functional traits. A saline-alkali-tolerant cultivar enriched bacterial genera such as Hydrogenophaga and Pseudomonas and fungal taxa including Chaetomium, which collectively stabilized co-occurrence networks, improved Na/K regulation, and increased yield under saline-alkali conditions (Lei et al., 2025). Functional predictions showed higher expression of ABC transporter and two-component system genes in its rhizosphere microbiome, indicating enhanced microbial stress-response capacity that supports plant tolerance.

Under water limitation, roots remodel microbiomes and exudates to support adaptation. Drought led to consistent enrichment of Actinobacteria and Bacillus in the rhizosphere of a drought-tolerant genotype, alongside increased organic acid and abscisic acid exudation and reduced amino acid exudation; these compositional changes were strongly correlated with shifts in bacterial genera such as Streptomyces that respond to hormone and metabolite profiles (Li et al., 2023). Comparative work on wild versus cultivated rice under contrasting water regimes showed that wild rice under non-irrigated conditions enriched nitrogen-assimilating and denitrifying functions and accumulated metabolites like L-phenylalanine and palmitic acid that may enhance water absorption and nutrient provisioning, supporting higher ecological adaptability to drought (Luo et al., 2025).

7.3 Effects on soil health improvement and yield formation

Enhancing rhizosphere biological activity contributes to soil health and yield formation through improved nutrient pools, enzyme activities, and microbial networks. In direct-seeded paddies, straw addition increased cellulase and protease activities, hydrolyzable N, and the abundance of bacterial groups such as Nitrospinae; these traits were positively correlated with grain yield, indicating that straw-driven shifts in rhizosphere bacteria and enzymes strengthen nutrient transformation and support higher productivity (Tang et al., 2024). Long-term winter cropping similarly improved soil organic C, total N, available N and P, and microbial biomass, while enhancing rhizosphere bacterial diversity clusters that contributed most to rice yield and its sustainability (Wang et al., 2025).

Manipulating microbial communities or inputs can directly boost yield while enhancing the rhizosphere environment. Biochar-based compound fertilizer increased rice biomass and N and P uptake, partly by raising redox potential and the potential difference between rhizosphere soil and root membranes, which reduced energy costs for nutrient accumulation and favored plant growth-promoting microbes (Chew et al., 2020). In ratoon rice, greater abundances of C and P cycling genes and higher β-glucosidase and acid phosphatase activities in the rhizosphere of the high-yielding variety were strongly associated with higher nutrient availability indices and ratoon yield, underscoring that functional, rather than purely structural, attributes of the microbiome are central to soil health and yield formation under intensive systems (Wang et al., 2025).

8 Case Study: Comparison of Root-Induced Soil Biological Activity under Different Water-Saving Rice Cultivation Systems

8.1 Differences in microbial communities between conventional flooding and alternate wetting and drying

Switching from continuous flooding (CF) to alternate wetting and drying (AWD) reshapes paddy microbial communities by altering redox conditions and plant-soil interactions. Whole-genome sequencing in fields with flooding irrigation (FI), AWD (AI), and ridge irrigation showed that AI and RI formed distinct bacterial communities from FI, with AI enriching Proteobacteria while reducing Actinobacteria in the upper soil profile (Wu et al., 2022). In an Italian field comparison, root-associated communities under AWD were enriched in aerobic and potentially plant growth-promoting groups such as Sphingomonadaceae and Rhizobiaceae, whereas anaerobic Deltaproteobacteria, Epsilonproteobacteria, and Firmicutes were depleted, indicating a shift toward more oxic, root-influenced assemblages on roots compared with CF (Hester et al., 2022).

Dry-wet cycles also affect specific functional guilds, especially methanogens and iron oxidizers. Under water-saving irrigation, the main methanogen Methanosarcina barkeri and genes for methanogenesis were reduced relative to FI, while genes for carbohydrate decomposition and nitrification were enhanced, suggesting a community better aligned with C and N cycling than with methane production (Wu et al., 2022). In a three-season field trial, AWD lowered soil Fe(II) but increased the copy number of Gallionella-related iron-oxidizing bacteria, with Fe(II) content negatively correlated with their 16S rRNA genes, showing that wet-dry redox fluctuations restructure iron-cycling communities at the strain level compared with CF (Watanabe et al., 2021).

8.2 Effects of intermittent irrigation on soil enzyme activities and nutrient transformation

Aerated regimes such as AWD increase nitrogen-transformation potential in rice rhizosphere compared with CF. Across tillering, heading and ripening, AWD (and flooding plus aeration) raised urease, protease and ammonia oxidase activities, while suppressing nitrate and nitrite reductase, leading to higher amoA and nifH gene abundances and lower nirS and nirK than under CF (Xu et al., 2022). The positive correlations between amoA/nifH and N-hydrolyzing enzymes, and between nir genes and nitrate reductase, indicate that AWD shifts enzymatic N cycling toward ammonification, nitrification and N fixation and away from denitrification, supported by higher microbial biomass C and N.

Intermittent irrigation also modifies organic N partitioning between rice and microbes. In a ^13C, ^15N-glycine labeling experiment, AWD increased dissolved oxygen and boosted both microbial growth and N-cycling enzymes relative to CF, improving rice growth and a nitrogen utilization index. At medium and high N supply, AWD enhanced direct plant uptake of labeled glycine while reducing microbial ^15N acquisition, and increased Gram-negative bacteria and fungi and the fungi:bacteria ratio in rhizosphere soils, showing that repeated wet-dry cycles reallocate organic N and restructure microbial competitors around roots (Cao et al., 2022).

8.3 Relationships among rhizosphere biological activity, rice yield, and water use efficiency

Water-saving cultivation systems that intensify rhizosphere biological activity can simultaneously increase yield and reduce water use. In a rice-rice system, the System of Rice Intensification, which includes younger seedlings, wider spacing, and intermittent irrigation, produced 12%-35% higher grain yields than best management practices while saving about 31%-37% irrigation water, and also increased rhizosphere dehydrogenase, microbial biomass C, and total bacteria, fungi and actinomycetes, indicating more active microbial communities under water-saving management (Gopalakrishnan et al., 2014). A four-year AWD field study likewise reported 5.2%-6.46% higher grain yields than monsoon flooding, together with 16%-54% increases in total and bioavailable N, P, K and several micronutrients, linked to enrichment of Bacillus, Pseudomonas, Rhizobium and other taxa that released pulses of macro- and secondary nutrients (Majumdar et al., 2023).

At finer scales, the strength and composition of rhizosphere activity help explain yield differences among managements and varieties. In ratoon rice, the higher-yielding cultivar showed significantly greater activities of C- and P-acquiring enzymes (β-glucosidase, acid phosphatase) and higher abundances of carbon fixation, degradation, and P-cycling genes, which were closely associated with available P, dissolved and easily oxidizable organic C, and final ratoon yield (Wang et al., 2025). In direct-seeded rice, straw incorporation increased cellulase and protease activities and hydrolyzable N, while adjusting rhizosphere bacterial structure; these enzyme-microbe-nutrient interactions correlated positively with grain yield, underscoring that enhanced rhizosphere biological functioning underlies productivity gains in improved rice systems (Tang et al., 2024).

9 Research Challenges and Future Perspectives

Multi-omics platforms now allow rhizosphere processes in rice to be characterized from molecules to communities, moving beyond descriptive surveys to mechanistic understanding. Integrated 16S rRNA sequencing and metabolomics in contrasting rice genotypes under drought revealed tight correlations between exudate profiles and bacterial community shifts, indicating that organic and amino acid exudation patterns can be linked statistically to specific taxa and functions. Similar integration of metabolomics and metagenomics in cadmium-contaminated fields distinguished low- and high-Cd cultivars by co-variation of metabolites, microbial taxa and nutrient-cycling capacities, showing how omics can identify microecosystem configurations that suppress contaminant uptake. Methodological reviews outline how marker-gene sequencing, metagenomics, metatranscriptomics, metaproteomics and metabolomics can be combined with network modelling to represent soil-plant-microbe systems as multi-layered functional entities. Multi-omics meta-analysis across legumes further demonstrates how developmental stage-specific “marker bacteria” and their expressed genes can be associated with plant growth, suggesting that similar cross-study mining in rice could reveal core growth-promoting consortia.

Evidence from rice and other crops indicates that variation in root architecture, exudation and internal aeration creates distinct microbial niches whose functions can complement root traits. Conceptual work on root ideotypes proposes that traits such as rooting depth, lateral branching, aerenchyma and root hair density modify oxygen, water and carbon rhizodeposition, thereby selecting microbial partners specialized in nitrogen transformation, phosphorus solubilization and water retention. Empirical studies show that rice genotypes differing in drought tolerance adjust exudate hormones and metabolites in ways that selectively enrich taxa such as Bacillus and Streptomyces, linking root plasticity to functional shifts in rhizosphere bacteria. Multi-omics analyses of low-Cd rice cultivars reveal rhizospheres enriched in nutrient-cycling genes and metabolite-microbe networks that immobilize Cd while supporting carbon, nitrogen and phosphorus cycling, illustrating a coordinated adjustment of root-zone metabolism and microbial functions. Ratoon rice with higher yields similarly hosts rhizosphere microbiomes enriched in carbon fixation, degradation and phosphorus cycling genes, and elevated nutrient-acquiring enzyme activities, showing that functional gene composition can synchronize with root nutrient demand during regrowth.

Green, high-efficiency systems aim to integrate root-microbe management with reduced external inputs to sustain yields and soil health. Long-term co-incorporation of green manure and rice straw increased double-rice yields, soil organic carbon, total nitrogen, microbial biomass and multiple C-, N- and P-cycling enzymes, demonstrating that organic inputs can build biological fertility while supporting productivity. Likewise, 16-year organic nutrient regimes combining vermicompost, crop residues and microbial inoculants in basmati systems substantially boosted microbial biomass, dehydrogenase activity, nutrient uptake and grain yield, highlighting the value of diversified organic sources and inocula. Systematic reviews emphasize that integrated nutrient management enhances microbial diversity, nutrient transformation and stress mitigation more than sole synthetic fertilization, offering a route to climate-resilient rice production with lower chemical dependence. Microbiome-engineering frameworks propose using beneficial bacteria, mycorrhizal fungi and synthetic communities to deliver biofertilization and stress tolerance, with success contingent on matching inoculants to soil properties and host genotypes. Multi-omics guided SynCom design under salinity further points toward climate-smart rice systems where rhizosphere engineering, root traits and input management are co-optimized for yield, resilience and environmental stewardship.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Cao X.C., Zhang J.H., Yu Y.J., Ma Q.X., Kong Y.L., Pan W.K., Wu L.H., and Jin Q.Y., 2022, Alternate wetting-drying enhances soil nitrogen availability by altering organic nitrogen partitioning in rice-microbe system, Geoderma, 424: 115993.
https://doi.org/10.1016/j.geoderma.2022.115993

Chen H., Yuan J.H., Chen G.L., Zhao X., Wang S.Q., Wang D.J., Wang L., Wang Y.J., and Wang Y., 2022, Long-term biochar addition significantly decreases rice rhizosphere available phosphorus and its release risk to the environment, Biochar, 4(1): 54.
https://doi.org/10.1007/s42773-022-00178-7

Chen K.H., Feng J., Bodelier P.L.E., Yang Z.M., Huang Q.Y., Delgado-Baquerizo M., Cai P., Tan W.F., and Liu Y.R., 2024, Metabolic coupling between soil aerobic methanotrophs and denitrifiers in rice paddy fields, Nature Communications, 15(1): 3471.
https://doi.org/10.1038/s41467-024-47827-y

Chen W., Gao Y., Yang J., Fan F.J., Zhang W., Li J., Zhou C.Z., Shi G., Tong F., and Fan G., 2022, Taxonomical and functional bacterial community selection in the rhizosphere of the rice genotypes with different nitrogen use efficiencies, Plant and Soil, 470(1-2): 111-125.
https://doi.org/10.1007/s11104-021-05170-x

Chen X.B., Xia Y.H., Rui Y.C., Ning Z., Hu Y.J., Tang H.M., He H.B., Li H.X., Kuzyakov Y., Ge T.D., Wu J.S., and Su Y.R., 2020, Microbial carbon use efficiency, biomass turnover, and necromass accumulation in paddy soil depending on fertilization, Agriculture, Ecosystems & Environment, 292: 106816.
https://doi.org/10.1016/j.agee.2020.106816

Chen Y., Xia A.Q., Zhang Z.J., Wang F., Chen J.H., Hao Y.B., and Cui X.Y., 2023, Extracellular enzyme activities response to nitrogen addition in the rhizosphere and bulk soil: a global meta-analysis, Agriculture, Ecosystems & Environment, 356: 108630.
https://doi.org/10.1016/j.agee.2023.108630

Chew J., Zhu L.L., Nielsen S., Graber E., Mitchell D.R.G., Horvat J., Mohammed M., Liu M.L., van Zwieten L., Donne S., Munroe P., Taherymoosavi S., Pace B., Rawal A., Hook J., Marjo C., Thomas D.S., Pan G.X., Li L.Q., Bian R.J., McBeath A., Bird M., Thomas T., Husson O., Solaiman Z., Joseph S., and Fan X.R., 2020, Biochar-based fertilizer: Supercharging root membrane potential and biomass yield of rice, Science of the Total Environment, 713: 136431.
https://doi.org/10.1016/j.scitotenv.2019.136431

De Bauw P., Mai T.H., Schnepf A., Merckx R., Smolders E., and Vanderborght J., 2020, A functional-structural model of upland rice root systems reveals the importance of laterals and growing root tips for phosphate uptake from wet and dry soils, Annals of Botany, 126(4): 789-806.
https://doi.org/10.1093/aob/mcaa120

Ding L.J., Cui H.L., Nie S.A., Long X.E., Duan G.L., and Zhu Y.G., 2019, Microbiomes inhabiting rice roots and rhizosphere, FEMS Microbiology Ecology, 95(5): fiz040.
https://doi.org/10.1093/femsec/fiz040

Dong H.Y., Sun H.Y., Chen C., Zhang M.M., and Deng D.X., 2023, Compositional shifts and assembly in rhizosphere-associated fungal microbiota throughout the life cycle of japonica rice under increased nitrogen fertilization, Rice, 16(1): 34.
https://doi.org/10.1186/s12284-023-00651-2

Fang W., Williams P.N., Zhang H., Yang Y., Yin D.W., Liu Z.H., Sun H.J., and Luo J.F., 2021, Combining multiple high-resolution in situ techniques to understand phosphorous availability around rice roots, Environmental Science & Technology, 55(19): 13082-13092.
https://doi.org/10.1021/acs.est.1c05358

Galindo-Castañeda T., Hartmann M., and Lynch J.P., 2024, Location: root architecture structures rhizosphere microbial associations, Journal of Experimental Botany, 75(2): 594-604.
https://doi.org/10.1093/jxb/erad421

Gopalakrishnan S., Kumar R.M., Humayun P., Srinivas V., Ratna B.K., Vijayabharathi R., Singh A., Surekha K., Padmavathi C., Somashekar N., Rao P.R., Latha P.C., Rao L.V., Babu V.R., Viraktamath B.C., Vinod G., Loganandhan N., and Babu V.R., 2014, Assessment of different methods of rice (*Oryza sativa* L.) cultivation affecting growth parameters, soil chemical, biological and microbiological properties, water saving and grain yield in rice-rice system, Paddy and Water Environment, 12(1): 79-87.
https://doi.org/10.1007/s10333-013-0362-6

Gu H.F., Wang X.Y., Zhang M.H., Jing W.Q., Wu H., Xiao Z.H., Zhang W., Gu J.F., Liu L.J., Wang Z.Q., Zhang J.H., Yang J.C., and Zhang H.C., 2023, The response of roots and rhizosphere environment to integrative cultivation practices in paddy rice, Journal of Integrative Agriculture, 23(6): 1879-1896.
https://doi.org/10.1016/j.jia.2023.06.031

Guo J., Ning H., Li Y.H., Xu Q., Shen Q.R., Ling N., and Guo S.W., 2024, Assemblages of rhizospheric and root endospheric mycobiota and their ecological associations with functional traits of rice, mBio, 15(3): e02733-23.
https://doi.org/10.1128/mbio.02733-23

Hester E.R., Vaksmaa A., Valè G., Monaco S., Jetten M.S.M., and Lüke C., 2022, Effect of water management on microbial diversity and composition in an Italian rice field system, FEMS Microbiology Ecology, 98(3): fiac018.
https://doi.org/10.1093/femsec/fiac018

Islam M.R., Price A.H., and Hallett P.D., 2024, Rhizosphere development under alternate wetting and drying in puddled paddy rice, European Journal of Soil Science, 75(4): e13533.
https://doi.org/10.1111/ejss.13533

Jat H.S., Datta A., Choudhary M., Sharma P.C., Dixit B., and Jat M.L., 2021, Soil enzymes activity: Effect of climate smart agriculture on rhizosphere and bulk soil under cereal based systems of north-west India, European Journal of Soil Biology, 103: 103292.
https://doi.org/10.1016/j.ejsobi.2021.103292

Lattacher A., Le Gall S., Rothfuss Y., Gao C., Harings M., Pagel H., Giraud M., Alahmad S., Hickey L.T., Kandeler E., and Poll C., 2025, Rooting for microbes: Impact of root architecture on the microbial community and function in top- and subsoil, Plant and Soil, 513(1): 333-351.
https://doi.org/10.1007/s11104-024-07181-w

Lau K.J.X., Chen B., Salammal M.S.T., Ramachandran S., and Naqvi N.I., 2025, Controlled irrigation suppresses methane emissions by reshaping the rhizosphere microbiomes in rice, Microbiology Spectrum, 14(2): e04929-24.
https://doi.org/10.1128/spectrum.04929-24

Lee H.J., Jeong S.E., Kim P.J., Madsen E.L., and Jeon C.O., 2015, High resolution depth distribution of Bacteria, Archaea, methanotrophs, and methanogens in the bulk and rhizosphere soils of a flooded rice paddy, Frontiers in Microbiology, 6: 639.
https://doi.org/10.3389/fmicb.2015.00639

Lei J., Gu H.F., Liu Z.Y., Hu X.X., Yu Z.W., Guan Q.J., Jin J., Liu X.J., Wang G.H., and Liu J.G., 2025, Recruitment of specific rhizosphere microorganisms in saline-alkali tolerant rice improves adaptation to saline-alkali stress, Science of the Total Environment, 963: 178413.
https://doi.org/10.1016/j.scitotenv.2025.178413

Li C., Sheng H.Y., Tan M., Dai H., Wang X.X., Xu H., Ding S.M., and Zhao G.J., 2025, Rhythmic radial oxygen loss enhances soil phosphorus bioavailability, Nature Communications, 16(1): 4413.
https://doi.org/10.1038/s41467-025-59637-x

Li C.X., Wang Y., Sun Q.Y., Chen M., Zhang C.B., Ding S.M., and Dai Z.C., 2024, Root-mediated acidification, phosphatase activity and the phosphorus-cycling microbial community enhance phosphorus mobilization in the rhizosphere of wetland plants, Water Research, 255: 121548.
https://doi.org/10.1016/j.watres.2024.121548

Li G.Y., Wang K.B., Qin Q.Q., Li Q., Mo F., Nangia V., and Liu Y., 2023, Integrated microbiome and metabolomic analysis reveal responses of rhizosphere bacterial communities and root exudate composition to drought and genotype in rice (*Oryza sativa* L.), Rice, 16(1): 19.
https://doi.org/10.1186/s12284-023-00636-1

Li J., Lin S.H., Wang Y., He H.B., and Fang C.X., 2022, Spatial-temporal distribution of allelopathic rice roots in paddy soil and its impact on weed-suppressive activity at the seedling stages, Frontiers in Plant Science, 13: 940218.
https://doi.org/10.3389/fpls.2022.940218

Li P., Tian Y., Yang K., Tian M.Y., Zhu Y.J., Chen X.H., Hu R.G., Qin T., Liu Y., Peng S.B., Yi Z.P., Liu Z.H., Ao H.J., and Li J., 2024, Mechanism of microbial action of the inoculated nitrogen-fixing bacterium for growth promotion and yield enhancement in rice (*Oryza sativa* L.), Advanced Biotechnology, 2(4): 32.
https://doi.org/10.1007/s44307-024-00038-4

Li S., Chen Y., Li T.Y., Yu F., Zhang Y.H., Liu K., Zhang H.C., Gu J.F., Yang J.C., and Liu L.J., 2022, Alternate wetting and moderate soil drying irrigation counteracts the negative effects of lower nitrogen levels on rice yield, Plant and Soil, 481(1): 367-384.
https://doi.org/10.1007/s11104-022-05644-6

Li X.Y., Li S., Jiang Y.F., Yang Q., Zhang J., Kuzyakov Y., Teng H.H., and Guan D.X., 2023, Multi-imaging platform for rhizosphere studies: Phosphorus and oxygen fluxes, Journal of Environmental Management, 351: 119763.
https://doi.org/10.1016/j.jenvman.2023.119763

Li Y., and Wang X.L., 2013, Root-induced changes in radial oxygen loss, rhizosphere oxygen profile, and nitrification of two rice cultivars in Chinese red soil regions, Plant and Soil, 365(1): 115-126.
https://doi.org/10.1007/s11104-012-1378-1

Li Z.F., Li Z.H., Letuma P., Zhao H., Zhang Z.X., Lin W.X., Chen H., and Lin W.X., 2018, A positive response of rice rhizosphere to alternate moderate wetting and drying irrigation at grain filling stage, Agricultural Water Management, 207: 26-36. https://doi.org/10.1016/j.agwat.2018.05.022

Li Z., Luo W.Z., Xie H., Mo C.H., Qin B., Zhao Y., Chen X., Zhang S.H., Zhao Y.L., Wang M., Yang Y., Cai J., Wang B.B., Liu X.Y., and Shi Y., 2025, Reovirus infection results in rice rhizosphere microbial community reassembly through metabolite-mediated recruitment and exclusion, Microbiome, 13(1): 1-19. https://doi.org/10.1186/s40168-025-02188-6

Liesack W., Schnell S., and Revsbech N.P., 2000, Microbiology of flooded rice paddies, FEMS Microbiology Reviews, 24(5): 625-645. https://doi.org/10.1111/j.1574-6976.2000.tb00563.x

Liu Y., Ge T.D., Ye J.S., Liu S.L., Shibistova O., Wang P., Wang J.K., Li Y., Guggenberger G., Kuzyakov Y., and Wu J.S., 2019, Initial utilization of rhizodeposits with rice growth in paddy soils: Rhizosphere and N fertilization effects, Geoderma, 338: 30-39. https://doi.org/10.1016/j.geoderma.2018.11.040

Liu Z.Y., Tang Z., Wang L., Wen L., Liang Y., Wang C.Y., and Wang H., 2025, The influence of planting method and short-term organic amendments on rhizosphere microbial communities in paddies: preliminary results, Agronomy, 15(3): 540. https://doi.org/10.3390/agronomy15030540

Luo Y., Xu X., Qiao R., Zhao R., Zhou Z.W., Li D.A., Wen Y., Song J., and Chen L.L., 2025, Comparative analysis of rhizosphere microbiomes of cultivated and wild rice under contrasting field water regimes, Microbiology Spectrum, 13(11): e00263-25. https://doi.org/10.1128/spectrum.00263-25

Majumdar A., Dubey P., Giri B., Moulick D., Srivastava A., Roychowdhury T., Bose S., and Jaiswal M., 2023, Combined effects of dry-wet irrigation, redox changes and microbial diversity on soil nutrient bioavailability in the rice field, Soil and Tillage Research, 232: 105752. https://doi.org/10.1016/j.still.2023.105752

Midya A., 2025, Present research priority on aerobic rice culture for sustainable rice production under the backdrop of shrinking water resource base: a review, Indian Journal of Agricultural Research, 59(3): 339-350. https://doi.org/10.18805/IJARe.A-6262

Midya A., Saren B.O., Dey J., Maitra S., Praharaj S., Gaikwad D.J., Gaber A., Alhomrani M., and Hossain A., 2021, Crop establishment methods and integrated nutrient management improve: Part II. Nutrient uptake and use efficiency and soil health in rice (*Oryza sativa* L.) field in the lower Indo-Gangetic Plain, India, Agronomy, 11(9): 1894. https://doi.org/10.3390/agronomy11091894

Nawaz A., Rehman A., Rehman H.U., Ahmad S., Siddique K.H.M., and Farooq M., 2022, Increasing sustainability for rice production systems, Journal of Cereal Science, 103: 103400. https://doi.org/10.1016/j.jcs.2021.103400

Pan J., Wang J.J., and Zhuang S.Y., 2022, Amino acid nitrogen trends in paddy soils under long-term rice cultivation in southeast coast of China, CATENA, 212: 106044. https://doi.org/10.1016/j.catena.2022.106044

Qi S.Y., Yang S.H., Xu Y.Q., Hu J., Qiu H.Y., Jiang Z.X., Zhang M.M., and Yu W.T., 2024, Enhanced available phosphorus in paddy fields applying biochar and water-saving irrigation together: the role of alkaline phosphomonoesterase-harboring microorganisms, Journal of Environmental Management, 371: 123260. https://doi.org/10.1016/j.jenvman.2024.123260

Qiao C.C., Yang J., Shao Q.Q., Fu J.Y., Zheng X.Y., Zhao J., Ren L.X., Wu W.L., and Wang J.K., 2025, Bio-organic fertilizers modulate therhizosphere bacterial community to improve plant yield in reclaimed soil, Frontiers in Plant Science, 2025, 16: 1660229. https://doi.org/10.3389/fpls.2025.1660229

Qu Y., Tang J., Liu B., Lyu H., Duan Y., Yang Y., Wang S., and Li Z., 2021, Rhizosphere enzyme activities and microorganisms drive the transformation of organic and inorganic carbon in saline-alkali soil region, Scientific Reports, 12(1): 1314. https://doi.org/10.1038/s41598-022-05218-7

Shenton M., Iwamoto C., Kurata N., and Ikeo K., 2016, Effect of wild and cultivated rice genotypes on rhizosphere bacterial community composition, Rice, 9(1): 42. https://doi.org/10.1186/s12284-016-0111-8

Soltani A., Jafarnode S., Zeinali E., Gherekhloo J., and Torabi B., 2024, Assessing aerobic rice systems for saving irrigation water and paddy yield at regional scale, Paddy and Water Environment, 22(2): 271-284. https://doi.org/10.1007/s10333-023-00966-2

Sun R., Zhang W., Liu Y., Yun W., Luo B., Chai R., Zhang C., Xiang X., and Su X., 2022, Changes in phosphorus mobilization and community assembly of bacterial and fungal communities in rice rhizosphere under phosphate deficiency, Frontiers in Microbiology, 13: 953340. https://doi.org/10.3389/fmicb.2022.953340

Tang Z., He N., Zhang L., Wang L., Gong D., Wang C., Wang H., Sui G.-M., and Zheng W., 2024, Straw and biochar application alters the structure of rhizosphere microbial communities in direct-seeded rice (*Oryza sativa* L.) paddies, Agronomy, 14(2): 316. https://doi.org/10.3390/agronomy14020316

Tang Z., Zhang L., He N., Gong D., Gao H., Fu L., Zhao M., Wang H., Wang C., Zheng W., and Zhang W.-Z., 2021, Soil bacterial community as impacted by addition of rice straw and biochar, Scientific Reports, 11(1): 22185. https://doi.org/10.1038/s41598-021-99001-9

Tian G., Husen Q., Li D., Wang Y., Bo Z., Li H., Niu Q., Qi D., and Zhou X., 2021, Little environmental adaptation and high stability of bacterial communities in rhizosphere rather than bulk soils in rice fields, Applied Soil Ecology, 169: 104183. https://doi.org/10.1016/j.apsoil.2021.104183

Wang C., Cheng B., Xiao Z., Ji Y., Zhang J., Zhou R., Yuan X.-Z., Kah M., Wang Z., and Xing B., 2025, Nanotechnology-driven coordination of shoot-root systems enhances rice nitrogen use efficiency, Proceedings of the National Academy of Sciences of the United States of America, 122(39): e2508456122. https://doi.org/10.1073/pnas.2508456122

Wang H., Zhou Q., Wang S., Zhang P., Wang L., Wang Z., Zhang L., and Huang G., 2025, Effects of long-term winter cropping on paddy rice yield, soil properties and rhizosphere bacterial community in Southern China, Field Crops Research, 322: 109734. https://doi.org/10.1016/j.fcr.2024.109734

Wang Y., Lou C., Geng X., Li S., Gao Y., Zhang S., Chen X., Zhang Y., Huang D., and Liang A., 2025, Effect of long-term tillage management on soil organic carbon fractions and enzyme activities in bulk and rhizosphere soils, Soil Use and Management, 41(3): e70109. https://doi.org/10.1111/sum.70109

Wang Z., Bai L., Dong S., Yang D., Tong Z., Zhong F., Zi H., Zeng Y., Chen M., Xu H., Zhang B., Lin W., and Zhang Z.-X., 2025, Regulatory role of rhizosphere microbial structure and function in yield formation of ratooning season rice, BMC Plant Biology, 26(1): 123. https://doi.org/10.1186/s12870-025-07915-7

Watanabe T., Katayanagi N., Agbisit R., Llorca L., Hosen Y., and Asakawa S., 2021, Influence of alternate wetting and drying water-saving irrigation practice on the dynamics of Gallionella-related iron-oxidizing bacterial community in paddy field soil, Soil Biology and Biochemistry, 152: 108064. https://doi.org/10.1016/j.soilbio.2020.108064

Wu J., and Li F., 2022, Microbial community structure and function in paddy soil as affected by water-saving irrigation mode, European Journal of Soil Biology, 113: 103450. https://doi.org/10.1016/j.ejsobi.2022.103450

Xu C., Xiao D.-S., Chen S., Chu G., Liu Y., Zhang X., and Wang D., 2022, Changes in the activities of key enzymes and the abundance of functional genes involved in nitrogen transformation in rice rhizosphere soil under different aerated conditions, Journal of Integrative Agriculture, 22(3): 923-934. https://doi.org/10.1016/j.jia.2022.08.036

Yi X., Yi K.-F., Fang K., Gao H., Dai W., and Cao L., 2019, Microbial community structures and important associations between soil nutrients and the responses of specific taxa to rice-frog cultivation, Frontiers in Microbiology, 10: 1752. https://doi.org/10.3389/fmicb.2019.01752

Yi X., Yuan J., Zhu Y.-H., Zhao Q., Fang K., Gao H., Dai W., and Cao L., 2018, Comparison of the abundance and community structure of N-cycling bacteria in paddy rhizosphere soil under different rice cultivation patterns, International Journal of Molecular Sciences, 19(12): 3772. https://doi.org/10.3390/ijms19123772

Yuan H., Zhu Z., Liu S.-L., Ge T., Jing H., Li B., Liu Q., Lynn T. M., Wu J., and Kuzyakov Y., 2016, Microbial utilization of rice root exudates: 13C labeling and PLFA composition, Biology and Fertility of Soils, 52(5): 615-627. https://doi.org/10.1007/s00374-016-1101-0

Yusuf A., Li M., Zhang S.Y., Odedishemi-Ajibade F., Luo R.F., Wu Y.-X., Zhang T.T., Ugya A.Y., Zhang Y., and Duan S., 2025, Harnessing plant-microbe interactions: strategies for enhancing resilience and nutrient acquisition for sustainable agriculture, Frontiers in Plant Science, 16: 1503730. https://doi.org/10.3389/fpls.2025.1503730

Zecchin S., Wang J., Martin M., Romani M., Planer-Friedrich B., and Cavalca L., 2023, Microbial communities in paddy soils: differences in abundance and functionality between rhizosphere and pore water, the influence of different soil organic carbon, sulfate fertilization and cultivation time, and contribution to arsenic mobility and speciation, FEMS Microbiology Ecology, 99(11): fiad121. https://doi.org/10.1093/femsec/fiad121

Zhong Y., Chi H., Wu T., Fan W., Su H., Li R., Jiang W., Du X., and Zhang Z., 2025, Diversity of rhizosphere microbial communities in different rice varieties and their diverse adaptive responses to saline and alkaline stress, Frontiers in Microbiology, 16: 1537846. https://doi.org/10.3389/fmicb.2025.1537846

Zhu K., Fu J., Zhang Y., Ren W., Zhang W., Gu J., Xu Y., Zhang H., Wang Z., Liu L., Zhang J., and Yang J., 2024, Root activity and rhizospheric bacteria in response to nitrogen management in rice (*Oryza sativa* L.), European Journal of Agronomy, 159: 127294. https://doi.org/10.1016/j.eja.2024.127294