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Review Article

Harnessing Wheat Rhizosphere Processes to Enhance Nutrient Use Efficiency

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Abstract

Wheat is among the most fertilizer-intensive cereal crop globally, yet a substantial proportion of applied fertilizers are lost through leaching, volatilization and immobilization, contributing to soil degradation, biodiversity loss and greenhouse gas emission while achieving only modest nutrient use efficiency often below 50%. Harnessing rhizosphere biology offers a promising pathway to reconcile yield demands with environmental sustainability. This review synthesizes current understanding of wheat rhizosphere structure and function, including root system architecture plasticity, root exudate chemistry and root-to microbiome signalling, that collectively shape microbial recruitment and nutrient dynamics. Wheat rhizosphere microbiome core functional groups include plant growth promoting rhizobacteria, arbuscular mycorrhizal fungi, phosphate-solubilizing microorganisms, diazotrophs and archaea through which they enhance nitrogen fixation, phosphorus mobilization and stress tolerance. Bio-fertilizers combinations and diversified cropping systems can reduce mineral fertilizer requirements by 20-50% while maintaining or improving wheat productivity. Emerging tools, including multi-omics profiling, synthetic microbial consortia, AI-guided precision fertilization and nano-fertilizer microbiome integration are advancing the field from empirical biofertilizer development toward rational, predictive microbiome engineering. Despite this progress, knowledge gaps persist regarding genotype-specific microbiome dynamics, temporal variability across growth stages and agroecological sites and the long-term ecological safety of novel interventions. Bridging these gaps through integrated field-based research will be essential for translating rhizosphere science into scalable, climate-smart nutrient management strategies that reduce wheat's reliance on synthetic fertilizers without compromising global food security.

Keywords: Environment, microbiome, nutrients, rhizosphere, wheat

1. Introduction

Globally, wheat cultivation, driven by increasing demand for production contributes to biodiversity loss, pollution of soil and water, greenhouse gas emissions because of mechanisation, fertilizer and pesticide usage. Application of excessive amounts of chemical fertilizers is beneficial neither to the crop nor to the soil, as a substantial proportion of the applied fertilizer is lost through volatilization and leaching before absorption by the crop plants. This overuse also leads to soil acidification, loss of microbial population in soil, decline in soil fertility and biodiversity, reduced nutrient use efficiency. Nutrient use efficiency refers to the ability of the crop to acquire nutrients from applied fertilizers. It is also partitioned into agronomic efficiency, physiological efficiency, recovery

efficiency and partial factor productivity (Rawal et al., 2022). Out of nitrogen fertilizer applied to wheat, only 48% is taken by the plants (Ladha *et al.,* 2016). For assessing the progress of the UN's Sustainable Developmental Goals, nitrogen use efficiency (NUE) is considered as an indicator (Zhang *et al.,* 2022). As food production continues to increase, the negative footprint created by intense agricultural practices must be reduced to mitigate the effects of climate change in the future (Martre *et al.,* 2024). Growing population necessitates increased agricultural production and productivity. However, balancing this demand with reduced chemical fertilizer application and environment sustainability remains the major scientific challenge in sustainable agriculture. In this context exploiting rhizosphere microorganisms in wheat offers a strategy to enrich the soil with reduced fertilizer input while maintaining yield potential and ensuring environment sustainability (Pan *et al.,* 2026).

The rhizosphere represents a key biological interface through which such sustainable interventions can be achieved. Rhizosphere region of soil and root zones has heterogeneous group of microorganisms which enhances the soil fertility, plant nutrient status and plant productivity (Chukwuneme and Babalola, 2025). Through root architecture modelling, immune system fortification and biosynthesis of metabolites such as siderophores, plant-microbe associations enhance nutrient bioavailability and micronutrient acquisition (Kozaeva *et al.,* 2024). Rhizosphere microorganisms perform diverse functions, including nitrogen fixing, phosphorus solubilizing, plant hormone synthesis, pathogen suppression, abiotic stress tolerance and growth promotion thereby enhancing plant nutrient uptake (Li *et al.,* 2025a; Haoran *et al.,* 2025). Wheat crop is a preferred model crop for rhizosphere research as it possesses a well-characterised root system comprising embryonic seminal and post embryonic nodal roots enabling efficient study of root-microbe interaction. Wheat roots exhibits a strong influence with rhizosphere function, releasing root exudates such as sugars, organic acids, fatty acids, poly alcohols into the soil which mediate plant-microbe interaction (Iannucci *et al.,* 2017; Fan *et al.,* 2018). This connection paves the way for healthy plant growth, development including stress tolerance and nutrient acquisition. Root architecture and exudate profiles are key determinants shaping the composition of the rhizosphere microbial community. This review summarizes current knowledge of wheat-rhizosphere interactions and their potential for reducing dependence on chemical fertilizer.

2. Wheat rhizosphere: Structural and chemical foundations

Rhizosphere is the small area of soil, a few millimetres from the root surface, that is immediately impacted by plant roots (Meena *et al.,* 2017). In terrestrial ecosystems, rhizosphere is one of the most biologically active interfaces where microorganisms, roots, soil, and ambient elements constantly interact (Goswami and Deka, 2022). Rhizosphere controls microbial recruitment, root development, nutrient uptake, and stress adaption in wheat (*Triticum aestivum* L.) (Kavamura *et al.,* 2021). The rhizosphere is a crucial target for enhancing sustainable wheat production because root architectural flexibility, exudate chemistry, physicochemical gradients, and root–microbiome communication all work together to affect nutrient usage efficiency as shown in Fig 1. (Zhou *et al.,* 2026).

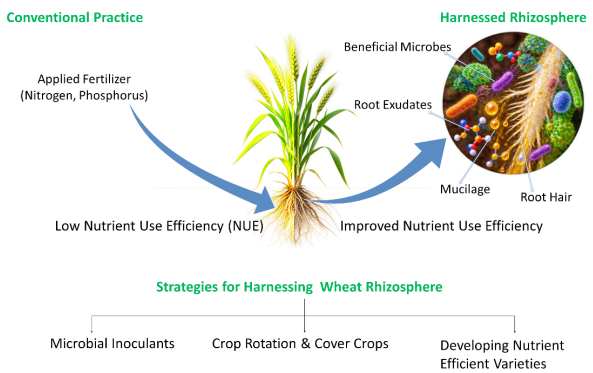

Fig 1. Conventional versus modern methods for increasing wheat yield.

2.1 Root system architecture and its plasticity under nutrient stress

Wheat's root system architecture (RSA) is defined by the spatial arrangement of primary, seminal, crown, lateral roots, as well as root hairs (Alrajhi *et al.,* 2024). Wheat can effectively explore diverse soil settings because of its exceptional RSA flexibility in response to nitrogen limitation (Joshi *et al.,* 2026). Phosphorus deficiency increases lateral root production and root hair density, thereby optimizing nutrient interception from the topsoil, whereas nitrogen deficiency typically encourages deeper rooting, longer roots, and higher root-to-shoot ratios (El Amrani, 2023). These responses are regulated by hormonal signalling pathways

involving auxin, cytokinin, ethylene, abscisic acid, together with nitrate/phosphate transporter mediated nutrient-sensing and networks (Jia *et al.,* 2022). By boosting soil exploration and lowering metabolic costs, root architectural characteristics have a direct impact on nutrient use efficiency (Lynch, 2022). As phosphorus is concentrated in the top soil layers, shallow root systems with extensive lateral branching enhance phosphorus uptake (Oo *et al.,* 2021). RSA traits are heritable and exhibit considerable genetic variation among wheat genotypes; thus, they represent promising targets for crop improvement. To facilitate the breeding of nutrient-efficient cultivars, recent genetic investigations have discovered quantitative trait loci (QTLs) and candidate genes affecting RSA plasticity in wheat (Chen *et al.,* 2022; H. Wang *et al.,* 2024; Alahmad *et al.,* 2019; Alrajhi *et al.,* 2024).

2.2 Root exudate composition

Root exudates comprise a chemically diverse group of compounds released into the rhizosphere through cell lysis, active secretion, and passive diffusion (Scavo *et al.,* 2019). According to Canarini *et al.* (2019), 10-40% of freshly fixed photosynthates can be translocated belowground, a sizable portion of which is released into the rhizosphere as exudates. Simple sugars (glucose, fructose, sucrose), amino acids (glutamate, glycine, serine), organic acids (malate, citrate, oxalate), vitamins, phytohormones, phenolics, flavonoids, coumarins, and benzoxazinoids are unique to cereals, constituting the major classes of root exudates as tabulated in Table 1. (Hou *et al.,* 2026). When compared to bulk soil, the rhizosphere displays sharp spatial gradients in physicochemical characteristics (Kuzyakov and Razavi, 2019). The rhizosphere experiences reduced redox potentials and oxygen depletion due to ongoing root and microbial respiration (Lacroix *et al.,* 2026). Organic acids are essential for nutrient mobilization because they increase phosphate solubility and acts as chelators of Fe^{3+}, Zn^{2+}, and Al^{3+}, amino acids serve as both chemoattractants and sources of nitrogen for rhizobacteria (Smirnova *et al.,* 2022). Benzoxazinoids, such as DIMBOA (2,4-Dihydroxy-7-methoxy-1,4-benzoxazin-3-one), HDMBOA (2-Hydroxy-4,7-dimethoxy-1,4-benzoxazin-3-one), and MBOA (6-Methoxybenzoxazolin-2-one) are typical secondary metabolites that serve as allelochemicals, antibacterial agents, and modulators of the microbial community composition in the rhizosphere. (Luo *et al.,* 2025; Hu *et al.,* 2018). Root uptake of nitrate and ammonium can alter the pH of the rhizosphere through differential release or uptake of protons and hydroxyl/bicarbonate ions (Rivero-Marcos *et al.,* 2026). The solubility of nutrients, especially phosphorus, iron, manganese, and zinc, is significantly affected by these localized pH variations (O'Kennedy, 2022).

Table 1. Major classes of rhizosphere-associated chemical signals and metabolites and their functional roles in wheat root and rhizosphere biology

Exudate class	Major compounds released by wheat	Primary function(s)	Contribution to Nutrient Use Efficiency (NUE)	References
Sugars (Carbohydrates)	Glucose, fructose, sucrose, maltose, arabinose, xylose	Carbon source for rhizosphere microbes; stimulate microbial growth	Enhances microbial mineralization of organic matter, increasing N and P availability	Ghatak *et al.,* 2025; Prudence *et al.,* 2021; Shaposhnikov *et al.,* 2023
Organic Acids	Malate, citrate, oxalate, fumarate, succinate, acetate, lactate, malonate	Chelate metal ions; acidify rhizosphere; solubilize phosphate	Mobilizes insoluble phosphorus, Fe, Zn and Mn; improves nutrient uptake under deficiency	Ghatak *et al.,* 2025; Prudence *et al.,* 2021; Wang *et al.,* 2024
Amino Acids	Glutamate, glutamine, aspartate, alanine, glycine, serine, valine, leucine, proline, lysine	Carbon and nitrogen source for microbes; signalling molecules	Supports beneficial microbes involved in nitrogen cycling and plant growth promotion	Ghatak *et al.,* 2025; Prudence *et al.,* 2021; Shaposhnikov *et al.,* 2023; Wang *et al.,* 2024
Phenolic Compounds	Ferulic acid, p-coumaric acid, vanillic acid, syringic acid, caffeic acid, salicylic acid	Antioxidant activity; microbial signalling; allelopathy	Shapes rhizosphere microbial community and suppresses pathogens, indirectly improving nutrient acquisition	Wang *et al.,* 2024

Benzoxazinoids (BXs)	DIMBOA, HDMBOA, DIBOA, MBOA, BOA	Defense against insects and pathogens; recruit beneficial microbes	Enrich beneficial bacterial communities involved in nutrient mobilization and disease suppression	Hazrati *et al.,* 2020
Flavonoids	Apigenin, luteolin, quercetin, kaempferol derivatives	Signalling compounds; antioxidant activity	Modulate microbial colonization and beneficial plant–microbe interactions	Ghatak *et al.,* 2025; Wang *et al.,* 2024
Fatty Acids & Lipids	Palmitic acid, stearic acid, oleic acid, linoleic acid	Carbon source; microbial signalling	Influence microbial community composition and nutrient cycling	Ghatak *et al.,* 2025; Prudence *et al.,* 2021; Wang *et al.,* 2024
Vitamins & Cofactors	Thiamine, riboflavin, biotin, nicotinic acid (trace amounts)	Support microbial metabolism	Enhance growth of beneficial rhizobacteria involved in nutrient transformation	Ghatak *et al.,* 2025; Wang *et al.,* 2024
Proteins & Enzymes	Acid phosphatase, proteases, peroxidases, glucanases	Hydrolyse organic nutrients; defense	Release inorganic phosphate and nitrogen from organic substrates	Staudinger *et al.,* 2022
Polysaccharides & Mucilage	Root mucilage, extracellular polysaccharides	Improve soil aggregation; retain moisture	Enhance nutrient diffusion, microbial habitat, and root–soil contact	Galloway *et al.,* 2020; Hosseini & Mosaddeghi, 2024
Phytohormones	Indole-3-acetic acid (IAA), abscisic acid (ABA), cytokinins, jasmonates (low concentrations)	Root development and stress signalling	Increase root surface area and nutrient absorption efficiency	Kumari *et al.,* 2019
Volatile Organic Compounds (VOCs)	Methanol, ethanol, acetaldehyde, terpenoids	Chemical communication; defense	Influence microbial interactions and nutrient-transforming microorganisms	Murata, 2025
Nucleotides & Nucleosides	Adenosine, uridine, ATP (trace levels)	Signalling molecules; microbial nutrition	Participate in rhizosphere signalling and microbial metabolism	Wang *et al.,* 2024

2.3. Root-to-Microbiome signalling

Plant roots and soil microbes communicate through a complex web of chemical signals (Sandhu *et al.,* 2025). According to Feng et al. (2021), root exudates function as chemoattractants which guide bacterial migration toward the rhizoplane via chemotaxis. Bacterial chemoreceptors identify sugars, amino acids, malate, citrate, and phenolic compounds, allowing beneficial taxa including *Pseudomonas, Bacillus, and Azospirillum* to colonize wheat roots (Gómez-Godínez *et al.,* 2023). Quorum sensing (QS), which relies on signalling molecules such as autoinducing peptides in Gram-positive bacteria and N-acyl homoserine lactones (AHLs) in Gram-negative bacteria, governs microbial populations interaction following colonization (Boban *et al.,* 2023). According to El-Sawy (2024), QS regulates biofilm formation, motility, antibiotic and siderophore biosynthesis, and the release of plant growth promoting compounds. Plants, in turn, are not merely passive recipients they can detect microbial QS molecules and incorporate them into immune signalling pathways to adjust defense responses (Shrestha *et al.,* 2020), while also actively secreting their own regulatory metabolites, such as benzoxazinoids, which selectively enrich beneficial microorganisms while suppressing pathogens (Baatsen *et al.,* 2026). In the wheat rhizosphere, this bidirectional communication supports microbiome formation, stress tolerance, and nutrient mobilization (Feng *et al.,* 2026).

3. Rhizosphere microbiome of wheat

Plants are increasingly recognized as establishing unique and dynamic microbial community in the soil surrounding

their roots, referred to as the rhizosphere (Philippot *et al.,* 2013; York *et al.,* 2016). The rhizosphere is a highly active region surrounding plant roots where root exudates (such as sugars, amino acids, organic acids, and secondary metabolites) attract and nourish microorganisms. The composition and functional potential of rhizosphere microbial communities are strongly influenced by plant genotype, soil nitrogen availability, and developmental stage (Chaparro *et al.,* 2014; Mohanram and Kumar, 2019; Li *et al.,* 2025 a,b). The rhizosphere microbiome is a key determinant of plant nutrition and stress adaptation through its involvement in nutrient transformation, phytohormone production, and pathogen inhibition (You *et al.,* 2024; Haoran *et al.,* 2025; Dutta *et al.,* 2025; Dwivedi *et al.,* 2025). The rhizosphere microbiome consists of a stable core microbiome comprising highly prevalent taxa that are consistently recruited across diverse environments and specialized in vital functions such as nutrient cycling, root signalling, and pathogen suppression. In addition, it includes a transient microbiome composed of flexible, non-obligate microbes whose presence is strongly shaped by short-term fluctuations in moisture, local chemistry, or stochastic environmental exposure. However, our understanding of the temporal dynamics of the wheat rhizosphere microbiome across developmental stages and its variability among different agroecological sites remains limited (Xu *et al.,* 2025). Therefore, a thorough understanding of plant-microbe interaction, identification of beneficial microbes and their functional roles, and the eventual harnessing of these beneficial functions to enhance sustainable agriculture without compromising the environmental quality. The wheat microbiome shows prominent variations with the developmental stage, tissue type, environmental conditions and genotype (Chen *et al.,* 2022). A diverse array of bacterial and fungal taxa, spanning multiple classes, genera, and species has been identified in association with wheat stems, leaves, roots, seeds, spikes, and rhizospheres, many of which play a beneficial role in growth and health. Harnessing the beneficial functions of these microbes is a promising method for enhancing the performance of wheat under different environmental stresses.

3.1. Diversification of microbes

A diverse and functionally active rhizosphere microbiome enhances beneficial plant-microbe interactions, improves nutrient acquisition, reduces nitrogen losses, and ultimately increases nitrogen use efficiency in crops. Under nitrogen-limited or variable nutrient conditions, beneficial microorganisms involved in biological nitrogen fixation, phosphorus solubilization, and plant growth promotion often become enriched (Zhang *et al.,* 2025). Moreover, the functional composition and the activity of the rhizosphere microbiome shift substantially between the flowering and grain-filling stages, critical periods for nutrient accumulation in wheat (Chen *et al.,* 2019). However, studies investigating genotype-specific shifts in rhizosphere microbiomes across contrasting nitrogen regimes remain limited, especially with respect to functionally important microbial groups. Beyond nitrogen-specific dynamics, rhizosphere microbiome composition is also shaped by broader host and environmental factors, as extensively documented across diverse agricultural systems.

A better understanding of these interactions could facilitate the identification of beneficial microbiomes for enhancing nitrogen use efficiency and supporting sustainable agricultural systems. Previous research has extensively investigated the composition, functional roles, and spatial variation of rhizosphere microbiomes associated with agricultural crops, as well as differences among host plant species (de Vries *et al.,* 2020). Several studies have demonstrated that rhizosphere microbial community composition differs significantly across geographic locations (Xiong *et al.,* 2021; Zhang *et al.,* 2024). For example, Yue et al. (2023) reported greater bacterial diversity in domesticated wheat than in wild wheat, whereas fungal diversity exhibited the opposite trend. Most studies have relied on either single growth-stage assessments or limited temporal sampling, leaving the dynamics of rhizosphere microbial composition, diversity, and functional changes throughout plant development across different environments largely unexplored (Xu *et al.,* 2025). Wheat, as one of the world's most vital grain crops, underpins both national economies and global food security. Regulating microbial communities through breeding or microbial inoculation to enhance crop yields represents a promising approach (Wen *et al.,* 2021). The plant microbiome comprises complex communities of bacteria, archaea, fungi and protists that interact with the host plant in different compartments (e.g. rhizosphere, endosphere and phyllosphere) (Turner *et al.,*2013). In

particular, the root-rhizosphere interface serves as a nexus of interactions through which plants acquire mineral nutrients and water, making it a key compartment that is key for future microbiome engineering solutions in agriculture (Bender *et al.*,2016).

The wheat rhizosphere harbours a diverse microbial community that plays a pivotal role in enhancing nitrogen use efficiency through complementary mechanisms involved in nutrient acquisition, transformation, and utilization (Dutta *et al.,* 2025). Plant growth-promoting bacteria (PGPB), including *Pseudomonas, Bacillus, Azospirillum, Rhizobium*, and Arthrobacter, enhance Nitrogen use efficiency through biological nitrogen fixation, phosphate solubilization, phytohormone production, siderophore secretion, and pathogen suppression, thereby stimulating root growth and improving nutrient uptake (Backer *et al.,* 2018; You *et al.,* 2024; Dwivedi *et al.,* 2025). Beneficial fungi, such as *Trichoderma, Penicillium, Mortierella*, and selected *Fusarium* species, contribute to organic matter decomposition, nutrient mineralization, phosphorus solubilization, and biological control of soil-borne pathogens, leading to increased nitrogen availability and improved nutrient acquisition (Haoran *et al.,* 2025; Dutta *et al.,* 2025). Likewise, arbuscular mycorrhizal fungi (AMF), particularly *Glomus* and *Rhizophagus,* establish mutualistic associations with wheat roots that expand the effective absorptive surface area, thereby enhancing the uptake of nitrogen, phosphorus, water, and micronutrients, especially under nutrient-limited conditions (Begum *et al.,* 2019; You *et al.,* 2024). Ammonia-oxidizing archaea (AOA) further regulate nitrogen cycling by catalysing the oxidation of ammonia to nitrite during nitrification, maintaining a continuous supply of plant-available nitrogen while influencing soil nitrogen dynamics (Prosser and Nicol, 2012). In addition, bacteriophages indirectly contribute to NUE by modulating bacterial community composition, suppressing pathogenic or competing bacterial populations, and maintaining a balanced rhizosphere microbiome that supports beneficial nitrogen-transforming microorganisms (Suttle, 2007; Dutta *et al.,* 2025). Collectively, these microbial groups function synergistically to improve nitrogen availability, nutrient uptake, root architecture, and nitrogen utilization efficiency, thereby enhancing wheat productivity while reducing reliance on synthetic nitrogen fertilizers (You *et al.,* 2024; Dwivedi *et al.,* 2025).

3.2. Methods to characterize microbiome

Microbiome-based approaches have emerged as valuable tools for improving wheat productivity by enabling the identification and exploitation of core microbiota and keystone taxa that regulate plant growth, nutrient acquisition, and stress resilience. Since the composition and function of rhizosphere microbial communities vary with environmental conditions, soil type, and geographical location, region-specific characterization is essential for developing effective microbiome-based interventions. Advances in high-throughput sequencing and multi-omics technologies, integrated with bioinformatics, have revolutionized the detection and functional characterization of plant-associated microbiomes, providing comprehensive insights into microbial diversity, community structure, metabolic activity, and ecological functions (Jain *et al.,* 2024). Among these approaches, 16S rRNA gene amplicon sequencing is the widely employed technique for bacterial community profiling, enabling the identification of bacterial taxa, estimation of community diversity, and comparison of microbial assemblages across different environments by targeting conserved regions of the 16S rRNA gene (Knight *et al.,* 2018).

Similarly, internal transcribed spacer (ITS) amplicon sequencing serves as the standard molecular marker for characterizing fungal communities due to its high taxonomic resolution and ability to distinguish fungal species (Nilsson *et al.,* 2019). While amplicon sequencing primarily provides taxonomic information, shotgun metagenomic sequencing enables comprehensive analysis of all microbial genomes present within a sample, facilitating the simultaneous identification of microbial taxa and functional genes involved in nutrient cycling, nitrogen metabolism, phytohormone biosynthesis, pathogen suppression, and abiotic stress adaptation (Quince *et al.,* 2017). To determine which microbial genes are actively functioning under specific environmental conditions, metatranscriptomicsanalyzes community-wide messenger RNA (mRNA), thereby revealing transcriptionally active metabolic pathways and dynamic plant–microbe interactions in the rhizosphere (Shi *et al.,* 2026).

Complementary to genomic and transcriptomic approaches, metabolomics employs analytical platforms such as liquid chromatography–mass spectrometry

(LC–MS) and gas chromatography–mass spectrometry (GC–MS) to identify root exudates and microbial metabolites that mediate microbial recruitment, nutrient mobilization, signaling processes, and stress responses within the rhizosphere (Jacoby *et al.,* 2021). In addition, culture-dependent isolation techniques remain indispensable for recovering viable microorganisms, enabling detailed physiological and biochemical characterization of beneficial taxa and experimental validation of plant growth-promoting traits, including biological nitrogen fixation, phosphate solubilization, phytohormone production, and biocontrol activity. These cultured isolates provide the foundation for developing microbial inoculants and synthetic microbial consortia for sustainable wheat production (Sarhan *et al.,* 2019). Together, the integration of amplicon sequencing, shotgun metagenomics, metatranscriptomics, metabolomics, and culture-based methods offers a comprehensive framework for deciphering the taxonomic composition, functional potential, metabolic activity, and ecological interactions of the wheat rhizosphere microbiome, thereby accelerating the development of microbiome-assisted strategies for enhancing nutrient use efficiency, stress tolerance, and crop productivity.

4. Mechanisms by which rhizosphere biology enhances nutrient availability

The rhizosphere is a highly dynamic zone of intense biological activity where plant roots interact with diverse microbial communities, including bacteria, fungi, archaea, and other microorganisms. These interactions regulate nutrient cycling, improve nutrient acquisition, and enhance plant growth through multiple biological and biochemical processes. Rhizosphere microorganisms play crucial roles in mobilizing soil nutrients that are otherwise unavailable to plants, thereby contributing to sustainable crop production and reducing dependence on chemical fertilizers (Philippot *et al.,* 2013).

4.1. Biological nitrogen fixation and associative diazotrophs in wheat

Unlike legumes, wheat cannot establish symbiotic nitrogen-fixing nodules; however, it forms beneficial associations with free-living and associative diazotrophic microorganisms that colonize the rhizosphere, rhizoplane, and root endosphere. These bacteria convert atmospheric nitrogen (N_2) into plant-available ammonium through the activity of the nitrogenase enzyme complex, thereby contributing to biological nitrogen fixation (BNF).

In addition to nitrogen fixation, associative diazotrophs function as plant growth-promoting rhizobacteria (PGPR) by producing phytohormones, improving root architecture, solubilizing nutrients, and enhancing plant tolerance to abiotic stresses. These combined activities improve nitrogen use efficiency (NUE), promote plant growth and biomass accumulation, and increase grain yield while reducing the dependence on synthetic nitrogen fertilizers. Major diazotrophic bacteria associated with wheat include *Azospirillumbrasilense, Azotobacter chroococcum, Herbaspirillumseropedicae, Azoarcus*spp., *Burkholderia* spp., *Kosakonia*spp., and *Paenibacillus*spp. (Backer *et al.,* 2018).

4.2. Phosphorus solubilization and mineralization

Although phosphorus (P) is abundant in agricultural soils, nearly 80–90% exists in insoluble inorganic complexes or organic forms that are inaccessible to plants (Sharma *et al.,* 2013). Phosphate-solubilizing microorganisms (PSMs) play a crucial role in enhancing phosphorus availability through phosphate solubilization and mineralization processes. These microorganisms secrete low-molecular-weight organic acids, including gluconic, citric, oxalic, malic, and succinic acids, which lower the rhizosphere pH and chelate calcium (Ca), iron (Fe), and aluminium (Al) ions, thereby releasing soluble orthophosphate from insoluble phosphate minerals (Sharma *et al.,* 2013; Rawat *et al.,* 2021).

Beyond inorganic phosphate solubilization, PSMs also mobilise phosphorus from organic soil pools, which constitute a significant proportion of total soil phosphorus, particularly in the form of phytate. PSMs produce extracellular enzymes such as phytases, acid phosphatases, and alkaline phosphatases, which hydrolyse organic phosphorus compounds into plant-available inorganic phosphate, thereby enhancing phosphorus acquisition and improving crop productivity (Richardson *et al.,* 2009). Common phosphate-solubilizing microorganisms associated with wheat include *Bacillus* spp., *Pseudomonas* spp., *Enterobacter* spp., *Penicillium* spp., and *Aspergillus* spp., all of which contribute to improved phosphorus use efficiency and sustainable nutrient management.

4.3. Mycorrhizal contributions to phosphorus and micronutrient uptake

Arbuscular mycorrhizal fungi (AMF) form mutualistic associations with the roots of most cereal crops, including wheat, enhancing plant growth and nutrient acquisition. Their extensive extraradical hyphal networks extend beyond the root depletion zone, allowing plants to access nutrients and water that are otherwise unavailable (Begum *et al.,* 2019). AMF are particularly effective in improving the uptake of relatively immobile nutrients such as phosphorus (P), zinc (Zn), iron (Fe), copper (Cu), and manganese (Mn), thereby increasing nutrient use efficiency under nutrient-deficient conditions.

In addition to nutrient acquisition, AMF enhance water uptake, improve root hydraulic conductivity, promote soil aggregation through glomalin production, and increase plant tolerance to drought, salinity, and soil-borne pathogens. Recent studies have also shown that AMF regulate the expression of plant nutrient transporter genes, further enhancing nutrient uptake and contributing to improved crop productivity and resilience under environmental stress (Begum *et al.,* 2019).

4.4. Root exudate driven microbial recruitment

Plants actively shape their rhizosphere microbiome by secreting a diverse range of root exudates, including sugars, amino acids, organic acids, phenolics, flavonoids, coumarins, and other specialized metabolites. According to Rolfe *et al.* (2019) under nutrient deficiency or biotic stress, plants alter the composition and quantity of these exudates to recruit beneficial microorganisms that enhance nutrient acquisition and stress tolerance, a process described as the "cry for help" hypothesis.

For instance, iron deficiency stimulates the release of coumarins and phenolic compounds that attract siderophore-producing bacteria, while phosphorus deficiency enhances the secretion of organic acids that promote phosphate-solubilizing microorganisms. Similarly, nitrogen limitation modifies carbon allocation to support nitrogen-fixing microbial communities. These beneficial microorganisms improve plant nutrition through biological nitrogen fixation, phosphorus solubilization, siderophore production, phytohormone synthesis, and pathogen suppression, ultimately enhancing nutrient use efficiency, plant growth, and resilience under nutrient-limited conditions (Philippot *et al.,* 2013).

4.5. Rhizosphere priming effects on soil organic matter turnover

The rhizosphere priming effect (RPE) refers to changes in the decomposition of soil organic matter triggered by root-derived carbon inputs and the associated stimulation of microbial activity (Kuzyakov and Razavi, 2019). Root exudates provide an energy source for soil microorganisms, promoting microbial growth, extracellular enzyme production, and the accelerated decomposition of organic matter. This process enhances the mineralization of essential nutrients such as nitrogen (N), phosphorus (P), and sulfur (S), thereby improving nutrient cycling and increasing nutrient availability for plant uptake (Kuzyakov and Razavi, 2019).

While moderate rhizosphere priming enhances nutrient acquisition and plant productivity, excessive priming can accelerate soil organic carbon loss, potentially compromising long-term soil fertility and carbon sequestration. Therefore, understanding the mechanisms regulating RPE is essential for developing sustainable agricultural systems that optimize nutrient use efficiency while maintaining soil health, ecosystem resilience, and long-term carbon storage (Philippot *et al.,* 2013).

5. Field level evidence: Reduced fertilizer strategies leveraging rhizosphere biology

The sustainability challenges connected with wheat production have become an impetus for the development of nutrient management technologies that reduce reliance on synthetic fertilizers while maintaining crop yield. Consequently, biological processes in the rhizosphere have become a major focus of recent research (Rawal *et al.,* 2024; Quille *et al.,* 2026). Beneficial microorganisms including PGPR, AMF, nitrogen fixing bacteria, and other microbial bio-stimulants enhance nutrient uptake through diverse mechanisms. These mechanisms collectively improve the capacity of wheat roots to explore the soil and take up nutrient from native soil and fertilizer derived sources. In addition, microbial activity improves soil aggregation, enhances nutrient mineralization, increases microbial biomass and enzymatic activity and enhance soil resilience to environmental stress (Zhang *et al.,* 2026; Imran and Ortas, 2025).

Numerous recent studies have demonstrated that rhizosphere-based interventions can substantially reduce fertilizer requirements without compromising crop

productivity and grain yield. Field experiments provide more ecologically realistic assessments than greenhouse or hydroponic studies, as they incorporate physiochemical characteristics climate variability, indigenous microbial populations, and agricultural practices. In different agro-ecosystems, microbial inoculants, organic supplements, integrated nutrient management systems, and diversified farming systems have greatly enhanced nutrient absorption, fertilizer efficiency, root growth, and soil biological activity. In most cases, these biological methods showed reduction in the use of mineral fertilizers by 40-50 percent, while maintaining or increasing the productivity of wheat plants (Kadhum *et al.,* 2021). The efficiency of these practices largely depends on their ability to synchronize nutrient supply with crop demand and to improve nutrient use efficiency within the soil-plant system.

The nitrogen fixation, phosphorus mobilization, root growth stimulation, and nutrient cycling by microorganisms enhance nutrient availability throughout the growing season thereby reducing nutrient loss and improving fertilizer use efficiency (Rakhmatova *et al.,* 2026). Combining microbial inoculations, organic inputs, and reduced fertilizer application can produce synergistic effects yielding outcomes superior to the sum of their individual impacts. This underscores the importance of an integrated approach to rhizosphere management rather than the application of elements in isolation. Biologically based nutrient management practices not only enhances agricultural productivity but also promote carbon sequestration, support microbiological community recovery, and contribute to the development of climate-smart wheat production systems (Yimer and Tarnawa, 2025).

5.1. Biofertilizer and microbial inoculant trials

The application of microbial biofertilizers can be regarded as an efficient way to improve nutrient use efficiency (NUE) in wheat cultivation and reduce fertilizer dependency. Among PGPR, *Bacillus, Pseudomonas, Azospirillum,* and *Azotobacter* species have shown positive effects on wheat under field conditions. PGPR application improves nitrogen and phosphorus uptake efficiency, enhances chlorophyll accumulation, and increases fertilizer use efficiency and reduces mineral fertilizer use by 20-30%, without compromising plant productivity. Moreover, AMF inoculation increases the absorptive surface area of roots via extraradical hyphae thereby enhancing phosphorus, zinc, and water uptake efficiency in low-fertility soil. AMF inoculation has been shown to reduce fertilizer usage by 30% (Qian *et al.,* 2024).

Recent research has focused increasingly on microbial consortia rather than individual inoculant application. Co-inoculation with PGPR, AMF, phosphate solubilizing bacteria, and potassium mobilizing microbes often produces synergistic effects, resulting in improved nutrient solubility, microbial abundance, and enhanced soil enzyme activity. The effectiveness of these microbial formulations have often shown greater effectiveness than individual strains in terms of yield, nutrient uptake and fertilizer use efficiency (Liu *et al.,* 2023).

Despite these positive outcomes, the efficiency of the microbial inoculants depends on the soil characteristics, climatic factors, wheat cultivars, and indigenous microbial populations. Nonetheless, field evidence collectively indicates that microbial biofertilizers represent a viable option for reducing chemical fertilizers application while maintaining wheat productivity (Shahwar *et al.,* 2023).

5.2. Organic amendments and microbial synergy

The combination of organic amendments with beneficial microbes has received much attention in recent years as an environmentally friendly approach to optimize nutrient use efficiency and lessen the reliance on chemical fertilizers in wheat cultivation. Organic amendments consisting of farmyard manure, compost, vermicompost, and biochar help in raising soil organic carbon, water retention, and aggregation, which provide a conducive environment for microbial growth and activity. Together with microbial inoculants such as PGPR, AMF, and phosphate-solubilizing bacteria (PSB), organic amendments contribute to the process of mineralization, nutrient availability, and nutrient synchronization, thus ensuring better nutrient uptake and wheat productivity (Ayamba *et al.,* 2023). Studies have shown that the combination of compost/manure with microbial inoculants increases soil enzyme activities, microbial biomass carbon, and rhizosphere microbial community abundance in comparison with individual treatments. These interactions facilitate the breakdown of organic matter and the release of nutrients in forms easily accessible to plants, thus contributing to increased fertilizer use efficiency. Moreover, microbial inoculants grow better on organic amendments, which provide

a favourable environment thereby improving their survival in the rhizosphere and enhancing plant-growth-promoting effects under field conditions (AlMethyeb *et al.,* 2023). Similarly, long-term experiments have revealed that the combination of organic and microbial nutrient management results in improved soil fertility through more than one growing season.

Improved levels of soil organic matter, nutrient cycling, and soil biological activity help in maintaining stable wheat yields and partial replacement of mineral fertilizers. In many production systems, it has been found that partial substitution of the recommended amount of NPK fertilizers by 20-40% with organic amendment along with microbial inoculants resulted in either maintenance or increase in grain yield and improved soil conditions while reducing the environmental impacts associated with excessive use of fertilizers (Xing *et al.,* 2025). Thus, this finding illustrates that synergy between the use of organic amendments and beneficial microbes is an important part of nutrient management in the rhizosphere of sustainable wheat. A related strategy involves combining reduced mineral fertilizer rates with biofertilizers or biostimulants to complement, rather than replace, mineral nutrition. Instead of substituting mineral fertilizers, this practice makes use of synergistic effects of beneficial microorganisms and biostimulants. Field trials have revealed that using PGPR, AMF, or phosphate solubilizers along with 75-80% of the recommended fertilizer dose has been proven to either maintain or increase wheat yield when compared with the use of the recommended dose of fertilizer (Sood *et al.,* 2019; Wang and Lu, 2020)

Biostimulants include humic substances, seaweed extracts, amino acids, and microbial metabolites. The Combined use of these biological products enhances nutrient absorption and transport, as well as root development and stress tolerance. This combination increases nutrient use efficiency, minimizes nutrient losses and improves the quality of grains, especially when nutrients are limiting factors (Ibn *et al.,* 2025). It is also noted that integrated nutrient management increases soil biological activity and fertilizer use efficiency while reducing production costs and the environmental impacts of wheat farming. Even though the extent of response may vary depending on soil properties and climate as well as other factors, the integration of biofertilizers and biostimulants with reduced rates of fertilizers provides a reasonable solution (Arinaitwe *et al.,* 2025).

5.3. Intercropping and rotation systems to enhance rhizosphere nutrient cycling

Diversified cropping systems, particularly intercropping and crop rotation, contribute significantly to improving rhizosphere-mediated nutrient cycling and reducing fertilizer requirements in wheat-based agroecosystems. This is achieved through changes in root structure and the diversification of root exudates and rhizosphere microflora which together enhance nutrient mobilization and recycling. Wheat-legumes intercropping systems have received considerable attention due to the symbiotic association between legumes and rhizobia, which contributes additional nitrogen input to the soil (Oburger *et al.,* 2022). Beyond nitrogen fixation, intercropping enhances rhizosphere chemistry through the secretion of organic acids, sugars, amino acids, and phenolic compounds by companion plant species, thereby encouraging the recruitment of beneficial microbes. Such exudates increase the solubility of phosphorus and micronutrients, enhance nutrient uptake efficiency, and reduce nutrient competition between the two crops.

Indeed, wheat-legumes intercropping is associated with improved nutrient efficiency, greater microbial richness, and higher fertilizer use efficiency compared with wheat monocropping (Karan *et al.,* 2026). Furthermore, crop rotation enhances rhizosphere activity by increasing soil organic matter content, microbial abundance and activity of enzymes involved in nutrients mineralization. Rotation with legumes benefits nitrogen supply and beneficial microbial population, while reducing soil-borne pathogen loads thereby promoting more effective nutrient cycling and stable productivity in subsequent years. Studies indicate that crop rotation involving diverse species improves soil health while minimizing fertilizer application, positioning it as a key element of climate-smart nutrient management as given in Table 2. (Hussain *et al.,* 2024; Basak *et al.,* 2025). Intercropping and crop rotation harness natural rhizosphere processes to improve nutrient cycling, soil biological fertility, and sustainable wheat productivity while minimizing fertilizer application. Combined with microbial inoculation and appropriate fertilization, these practices represent a promising strategy for environmentally sustainable wheat production.

Table 2. Comparative summary of rhizosphere-based strategies for improving nutrient use efficiency in wheat

Strategy	Typical fertilizer reduction achieved	Yield impact	Major rhizosphere mechanism	References
PGPR inoculation	20-30% N and P	Maintained or increased (5-15%)	Biological N fixation, phytohormone production, phosphate solubilization, improved root growth	Dawlatzai *et al.,* 2017; Schütz *et al.,* 2018
AMF inoculation	20-50% P	Maintained or increased	Hyphal-mediated nutrient acquisition, improved P and micronutrient uptake	Schütz *et al.,* 2018
Organic amendments and beneficial microbes	20-40% NPK	Increased or maintained	Enhanced nutrient mineralization, microbial biomass, soil enzyme activity	Luo *et al.,* 2018; Jiang *et al.,* 2026
Reduced fertilizer and biofertilizers/ biostimulants	20-25% fertilizer	Comparable or higher yield	Improved nutrient uptake, fertilizer recovery efficiency, enhanced root physiology	Schütz *et al.,* 2018; Jiang *et al.,* 2026
Wheat-legume intercropping	25-50% N	Comparable or increased system productivity	Biological nitrogen fixation, complementary nutrient uptake, root exudate-mediated facilitation	Bedoussac *et al.,* 2015
Wheat–legume crop rotation	20-40% N	Stable or increased yield	Residual nitrogen contribution, improved microbial diversity and nutrient cycling	Nan *et al.,* 2026; Pandit *et al.,* 2026

6. Emerging tools and approaches

6.1. Multi-omics integration

The wheat rhizosphere is a highly active biological zone where roots, microorganisms, and soil interact to enhance nutrient cycling and plant productivity. Traditional microbiological methods mainly characterize microbial diversity but provide limited insights into the functional mechanisms of nutrient acquisition. The advent of multi-omics technologies including metagenomics, metatranscriptomics, metaproteomics, and metabolomics has significantly advanced rhizosphere research, enabling comprehensive analysis of microbial communities and their roles in plant-microbe interactions. Metagenomics, particularly through high-throughput sequencing, has identified diverse microorganisms including nitrogen-fixing bacteria and mycorrhizal fungi that enhance nutrient availability and plant growth (Rajguru *et al.,* 2024; Fan *et al.,* 2018). However, metagenomics reveals genes related to nitrogen fixation and phosphorus solubilization without differentiating between active and inactive microorganisms. To address this, metatranscriptomics and metaproteomics are utilized to identify actively expressed genes and enzymes involved in key processes like nitrogen fixation and nutrient transport. These complementary approaches facilitate the detection of metabolically active microorganisms, moving beyond mere diversity description. Additionally, metabolomics provides insights into the variety of metabolites produced by microbes and plant roots, which serve as chemical signals for nutrient mobilization and microbial recruitment. Certain compounds, such as sugars and organic acids, promote beneficial microbial growth and nutrient solubilization, indicating that the interplay of metabolites is essential for microbial community dynamics and nutrient uptake in wheat rhizosphere. While carbon-rich exudates promote the growth of PGPR, greater secretion of citrate and malate improves phosphate solubilization by beneficial microbes in phosphorus-deficient environments. A recent metabolomic study of perennial wheat identified more than 2,500 metabolites linked to roots and the rhizosphere, indicating that plant and microbe-derived metabolites are crucial for microbial community assembly, stress tolerance, and nutrient uptake, finding that may offer valuable comparative insights for annual wheat systems (Giannelli *et al.,* 2025).

6.2. Synthetic microbial consortia (SynCom) design for wheat

The increasing demand for sustainable wheat production is driving the advancement of synthetic microbial consortia (SynComs) as a more effective alternative to traditional single-strain biofertilizers, such as those based on *Azospirillum, Bacillus, or Pseudomonas*. While single strains may excel in laboratory settings, they often perform inconsistently under field conditions due to competition from native soil microorganisms and variable environmental factors. (Alzate Zuluaga *et al.,* 2024). In contrast, SynComs consist of diverse, compatible microbial communities that enhance various plant functions, including biological nitrogen fixation, phosphorus solubilization, micronutrient mobilization, phytohormone production, pathogen suppression, and stress tolerance. This ecological model better simulates the natural wheat rhizosphere microbiome, yielding greater functional stability compared to single-strain inoculants. SynComs specifically target core microbiome members and keystone taxa that effectively colonize wheat roots and contribute to nutrient cycling. Using metagenomics, metabolomics, and microbial network analysis, researchers can now identify microorganisms that synergistically interact rather than compete. Typically, wheat SynComs include nitrogen-fixing bacteria (e.g., *Azospirillum, Herbaspirillum*), phosphate-solubilizing bacteria (e.g., *Bacillus, Pseudomonas*), potassium-mobilizing bacteria, siderophore-producing microorganisms, arbuscular mycorrhizal fungi (AMF), and beneficial fungi like *Trichoderma*, which together improve nutrient availability and root development. Such approaches illustrate the broader potential to design tailored microbial communities that enhance multiple plant functions simultaneously beyond disease suppression alone. Recent advancements in microbiome engineering integrate multi-omics data with computational biology, employing artificial intelligence and microbial interaction networks to predict microbial compatibility, identify keystone species, and optimize consortium design prior to field trials (Mehlferber *et al.,* 2024). The Design Build Test Learn (DBTL) framework facilitates the swift development of stable microbial communities with enhanced functional performance across various environments. These predictive methodologies signify a major shift from traditional empirical biofertilizer development to a more rational and predictive approach to microbiome engineering, aimed at enhancing sustainable wheat production.

6.3. Precision or site-specific fertilization informed by rhizosphere microbiome status

Precision agriculture enhances nutrient use efficiency (NUE) in wheat by optimizing fertilizer applications tailored to crop demand, soil characteristics, and rhizosphere biology. Traditional methods often apply uniform rates that ignore variability in nutrient availability and microbial activity in soils, leading to over-fertilization and under-fertilization challenges. Site-specific nutrient management (SSNM) integrates soil analysis, crop nutrient status, remote sensing, GIS, GPS, artificial intelligence (AI), and microbiome data to improve fertilizer efficiency and minimize environmental impacts. Recent advances in microbiome studies have expanded precision fertilization beyond standard soil tests, showcasing how beneficial microorganisms facilitate nutrient availability through processes like nitrogen fixation and phosphorus solubilization. High-throughput sequencing now aids in identifying microbial markers linked to soil fertility, enhancing the accuracy of nutrient predictions for fertilization strategies. (Rajguru *et al.,* 2024) Monitoring technologies, including satellite imagery and UAVs, facilitate real-time assessments of crop nutritional status via vegetation indices, enabling targeted fertilizer applications to address deficiencies effectively. AI and machine learning can play critical roles in precision nutrient management by analysing extensive datasets from various sources to optimize fertilizer application timing and predict yield responses under different conditions. Variable-rate technology (VRT) employs GPS and GIS to adjust fertilizer applications based on nutrient variability, further refining nutrient management strategies. Despite these advancements, barriers to adopting microbiome-informed fertilization remain, including high costs, the need for advanced technologies, and insufficient microbial data integration into decision-support systems. The variability of microbial communities across soils and climates complicates standardized recommendations. Future research must focus on long-term field experiments and the integration of microbiome profiling with AI models to establish effective, sustainable nutrient management practices for wheat production.

6.4. Nanofertilizers and enhanced-efficiency Fertilizers

Nanofertilizers and enhanced-efficiency fertilizers (EEFs) have emerged as innovative nutrient delivery systems that improve fertilizer use efficiency while minimizing environmental losses. Unlike conventional fertilizers, nanofertilizers possess a high surface area, controlled-release properties, and enhanced nutrient availability, enabling gradual nutrient release that better synchronizes with crop demand. Similarly, enhanced-efficiency fertilizers, including polymer-coated, sulfur-coated and urease or nitrification-inhibitor-treated fertilizers, reduce nitrogen losses through ammonia volatilization, nitrate leaching, and denitrification. Beyond improving nutrient delivery, these advanced fertilizers also influence the biological processes occurring in the wheat rhizosphere by modifying root exudation patterns, microbial community composition, and enzyme activities involved in nutrient cycling. Recent studies have shown that nano-zinc, nano-iron, and nano-hydroxyapatite fertilizers can stimulate the abundance of plant growth-promoting rhizobacteria (PGPR), arbuscular mycorrhizal fungi (AMF), and phosphate-solubilizing microorganisms, thereby enhancing nutrient mobilization and root nutrient uptake (Saurabh *et al.,* 2024; Dimkpa *et al.,* 2017). Furthermore, the integration of nano-fertilizers with beneficial microbial inoculants has demonstrated synergistic effects on root growth, chlorophyll synthesis, antioxidant activity, and nitrogen and phosphorus uptake in cereal crops, suggesting that nanotechnology and rhizosphere microbiome engineering can complement each other to improve nutrient use efficiency and crop productivity. Nevertheless, long-term studies are still required to evaluate the persistence, transformation, and ecological safety of nanoparticles in agricultural soils, particularly their effects on non-target microbial communities and soil ecosystem functions. Therefore, future research should focus on developing environmentally safe nano-fertilizer formulations that are compatible with beneficial rhizosphere microorganisms and can be integrated with precision nutrient management strategies to achieve sustainable wheat production (Kah *et al.,* 2018; Saurabh *et al.,* 2024).

7. Conclusion

The wheat rhizosphere represents a biologically rich and functionally versatile system whose exploitation offers a scientifically credible route toward reducing chemical fertilizer dependency without sacrificing productivity. Across root architecture plasticity, exudate driven microbial recruitment, and the diverse metabolic capabilities of core and transient microbiome members. Here the review highlights consistent evidence that rhizosphere-based interventions ranging from single-strain biofertilizer to multi-strain consortia, organic amendment synergies and diversified cropping systems can deliver 20-50% reductions in mineral fertilizer use while maintaining yield and improving soil health. However, the efficacy of these strategies remains context dependent, shaped by soil type, climate, wheat genotype and indigenous microbial populations, underscoring the need for region and cultivar specific optimization. Emerging technologies, particularly multi-omics integration, rationally designed synComs, AI-assisted precision fertilization, and nanofertilizers and microbiome co-formulations are poised to accelerate this transition from empirical to predictive microbiome engineering. Realizing the full potential of rhizosphere based nutrient management will require sustained investment in long-term, multi-site field trials, deeper characterization of genotype-by-microbiome interactions and careful evaluation of the ecological safety of novel formulations. With the continued interdisciplinary research, harnessing wheat rhizosphere processes can become a central pillar of climate-smart, sustainable wheat production systems.

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Conflict of interest

The authors declare no conflict of interest

Author contributions

Conceptualization and overall planning, R.V., Rinki; writing-original draft, R.V., Kiran, V.S., P.R., A., Z.W.; literature search, P.R., Anjali., Z.W., A.K., Y.K.; figures and tables, V.S., Kiran; manuscript drafting and editing, R.V., Rinki, V.P.; supervision and overall guidance, A.G. and R.T. All authors have read and agreed to the published version of the manuscript.

Ethical compliance statement

NA

Declaration on the use of Generative AI or AI-assisted technologies

The authors declare that no generative AI or AI-assisted technologies were used in the preparation of this manuscript. All text, data interpretation, and analysis were conducted entirely by the authors.

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