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FROM SOIL METAGENOMICS TO FUNCTIONAL MULTI-OMICS: DECIPHERING PLANT–SOIL–MICROBIOME INTERACTIONS FOR SUSTAINABLE AGRICULTURE – A REVIEW

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ABSTRACT
Sustainable agriculture requires a comprehensive understanding of the molecular mechanisms through which soil microorganisms regulate ecosystem functioning and plant productivity. While metagenomics has significantly advanced the characterization of microbial diversity and functional potential, it provides limited insight into the biological activities occurring under dynamic environmental conditions. Functional multi-omics, integrating metagenomics, metatranscriptomics, metaproteomics and metabolomics, overcomes this limitation by linking microbial genetic potential with active biological processes. This integrated systems biology approach provides unprecedented insights into plant-soil-microbiome interactions and their roles in nutrient cycling, disease suppression, abiotic stress tolerance and carbon sequestration. Advances in functional multi-omics have elucidated the molecular mechanisms governing microbial community assembly, rhizosphere communication and ecosystem functioning, enabling the identification of key microbial taxa, functional genes, proteins and metabolites associated with sustainable agricultural processes. These discoveries have accelerated the development of microbiome engineering strategies, microbiome informed crop improvement, synthetic microbial communities and next generation microbial biofertilizers aimed at enhancing nutrient-use efficiency, improving crop resilience and reducing dependence on synthetic agrochemicals. Despite these advances, challenges related to experimental standardization, multi-omics data integration, computational analyses, field scale validation and regulatory frameworks continue to constrain large scale agricultural implementation. Future integration of functional multi-omics with artificial intelligence, precision agriculture, remote sensing and predictive ecological modelling is expected to facilitate site-specific microbiome management and climate-smart farming practices. Overall, functional multi-omics provides a transformative framework for bridging microbial diversity with ecosystem function, offering new opportunities to improve soil health, agricultural productivity and environmental sustainability.

KEYWORDS: Functional multi-omics; Soil microbiome; Metagenomics; Metatranscriptomics; Metaproteomics; Metabolomics; Microbiome interactions; Sustainable agriculture.

1. INTRODUCTION

Agriculture is facing unprecedented challenges in meeting the food demands of a rapidly growing global population while simultaneously addressing climate change, soil degradation, biodiversity loss and the environmental consequences associated with excessive dependence on synthetic fertilizers and pesticides (Shahmohamadloo et al., 2021). Although conventional agricultural intensification has substantially increased crop productivity over recent decades, it has also accelerated soil nutrient depletion, disrupted beneficial microbial communities, reduced ecosystem resilience and contributed to environmental pollution (Sudarshan et al., 2024). Consequently, there is an increasing global emphasis on developing sustainable agricultural systems that maintain high productivity while preserving soil health, conserving ecosystem functions and minimizing environmental impacts.

Central to this transition is the soil microbiome, which has emerged as a fundamental determinant of agricultural sustainability owing to its critical role in nutrient cycling, organic matter decomposition, soil carbon sequestration, disease suppression and plant adaptation to environmental stresses (Madhulika et al., 2025). Within the rhizosphere, complex interactions among plant roots, soil microorganisms and their surrounding environment create a highly dynamic biological interface that regulates plant growth and productivity. Beneficial microorganisms promote biological nitrogen fixation, phosphorus solubilization, phytohormone production, induced systemic resistance and tolerance to abiotic stresses, thereby reducing reliance on chemical inputs while enhancing crop performance (Feng

et al., 2026). Consequently, understanding the molecular mechanisms governing these interactions has become a major research priority for developing climate resilient and resource efficient agricultural systems.

The rapid advancement of high sequencing technologies has revolutionized our understanding of soil microbial communities. Initial investigations relied primarily on culture dependent methods or marker gene sequencing to characterize microbial diversity, whereas the advent of shotgun metagenomics enabled comprehensive characterization of both microbial taxa and their functional genes (Sardar et al., 2024). Despite this significant progress, metagenomics primarily reveals the genetic potential of microbial communities and provides limited insight into the biological processes that are actively occurring under specific environmental conditions. Because the presence of functional genes does not necessarily indicate their expression or contribution to ecosystem functioning, there is an increasing need for complementary approaches capable of capturing microbial activity across multiple molecular levels (Jansson & Hofmockel, 2018).

To overcome these limitations, functional multi-omics has emerged as a powerful systems biology framework that integrates metagenomics, metatranscriptomics, metaproteomics and metabolomics to bridge the gap between microbial genetic potential and realized biological function (Zhang et al., 2010). By simultaneously investigating gene content, transcriptional activity, protein expression and metabolite production, functional multi-omics provides a comprehensive understanding of plant-soil-microbiome interactions and the molecular mechanisms underlying nutrient cycling, stress adaptation, disease suppression and carbon sequestration (Li et al., 2026). Rather than serving solely as a descriptive tool for microbial community profiling, these integrated approaches enable mechanistic and predictive insights that can guide precision agricultural management and microbiome based interventions.

Recent advances in functional multi-omics have transformed our understanding of plant-soil-microbiome interactions by integrating microbial genetic potential with functional activity. The roles of metagenomics, metatranscriptomics, metaproteomics and metabolomics in elucidating key processes underlying nutrient cycling, disease suppression, abiotic stress tolerance and carbon sequestration are examined, together with their applications in microbiome engineering, crop improvement and microbial biofertilizer development. Current challenges and future research directions are also discussed to highlight the potential of functional multi-omics in advancing resilient and sustainable agricultural systems.

2. The Soil Microbiome: Foundation of the Tripartite System

The successful application of functional multi-omics in sustainable agriculture first requires an understanding of the biological complexity of the soil microbiome. A gram of agricultural soil can harbour thousands of bacterial and archaeal taxa alongside a rich assemblage of fungi, protists and viruses, making soil among the most microbially diverse habitats on Earth (Bahram et al., 2018). These microorganisms form intricate ecological networks with plants and soil, creating a tripartite system that underpins nutrient cycling, plant productivity and overall soil health (Pandit et al., 2026).

Bacteria and archaea dominate numerically and drive most nutrient transformation reactions, whereas fungi including both saprotrophic decomposers and mycorrhizal symbionts contribute disproportionately to organic matter turnover and soil structure formation (Berg et al., 2020). Protists regulate bacterial populations through grazing, thereby influencing nutrient mineralization, while soil viruses shape microbial community composition through lysis and horizontal gene transfer (Trivedi et al., 2020). This remarkable microbial diversity is particularly concentrated within the rhizosphere, the narrow zone of soil directly influenced by plant roots, where microbial abundance and metabolic activity can be several orders of magnitude greater than those observed in bulk soil (Upadhyay et al., 2022).

Describing soil microorganisms solely on the basis of taxonomy provides only limited insight into their ecological roles. From an agronomic perspective, it is therefore more informative to classify microorganisms according to their functional guilds rather than their taxonomic identity (Table 1). Furthermore, because the majority of soil microorganisms remain unculturable under laboratory conditions, the soil metagenome which represents the collective genetic repertoire of the microbial community, constitutes a vast and largely unexplored reservoir of biosynthetic and metabolic potential (Berg et al., 2020).

Table 1. Key functional microbial guilds in the plant-soil-microbiome system

Functional Guild	Representative Taxa	Primary Agronomic Function	Reference
Nitrogen fixers (symbiotic)	Rhizobium, Bradyrhizobium, Sinorhizobium	Root-nodule symbiosis converting N_2 to plant available ammonium	(Chen & Zhou, 2024)
Nitrogen fixers (free-living)	Azotobacter, Azospirillum	Non-symbiotic biological nitrogen fixation in the rhizosphere	(Smercina et al., 2019)
Phosphate solubilizers	Pseudomonas, Bacillus, Penicillium	Mineralization of organic P and solubilization of mineral bound P	(Sun et al., 2026)

PGPR	Pseudomonas fluorescens, Bacillus subtilis	Phytohormone modulation, siderophore production, ACC deaminase activity	(Sivasakthi et al., 2014)
Mycorrhizal fungi	Arbuscular mycorrhizal fungi (Glomeromycotina)	Extended nutrient (esp. P) and water uptake, rhizosphere structuring	(Miransari, 2013)
Biocontrol agents	Streptomyces, Trichoderma, antagonistic Pseudomonas	Antibiosis, competition and induced systemic resistance	(Mahapatra et al., 2024)

Importantly, comparative metagenomic studies have demonstrated that microbial taxonomic composition and functional gene content are often only weakly correlated (Manor & Borenstein, 2017). Functional genes involved in key ecosystem processes, such as phosphorus solubilization and nitrification, are distributed across taxonomically diverse microorganisms, resulting in substantial functional redundancy (Siles et al., 2022). Consequently, critical soil functions can often be maintained despite considerable shifts in microbial community composition arising from changes in agricultural management or environmental conditions (Shaffer et al., 2022). This observation highlights that understanding ecosystem functioning requires greater emphasis on microbial functional capacity than on taxonomic composition alone.

The assembly of soil microbial communities is likewise governed by multiple interacting factors. Abiotic filters including soil type, pH, organic matter content, land use history and management practices, determine the pool of microorganisms capable of surviving within a given soil environment (Upadhyay et al., 2022). Superimposed on these environmental filters is host mediated selection, whereby plants actively recruit a subset of the surrounding microbial community into the rhizosphere and endosphere through root derived chemical signals (Pacheco-Moreno et al., 2024). These selective interactions establish the biological foundation of the plant-soil-microbiome continuum, influencing microbial community assembly and the functional processes that sustain soil health and crop productivity.

3. Soil Metagenomics: Cataloguing the Genetic Potential of Soil Microbiomes

3.1 Principles and Workflow

Characterizing the immense diversity and functional potential of soil microbial communities is fundamental to understanding their roles in ecosystem functioning and sustainable agriculture. Because the vast majority of soil microorganisms cannot be cultured using conventional laboratory techniques, culture independent molecular approaches have become indispensable for studying soil microbial communities (Rincon-Florez et al., 2013). Among these, soil metagenomics has emerged as one of the most powerful tools for comprehensively exploring the taxonomic composition and genetic repertoire of complex microbial ecosystems (Ejaz et al., 2024).

Soil metagenomics involves sequencing the total DNA extracted directly from soil or rhizosphere samples, enabling comprehensive characterization of microbial communities without the need for cultivation (Sabale et al., 2019). Unlike amplicon-based sequencing, which targets conserved marker genes such as the 16S rRNA gene primarily for taxonomic identification, shotgun metagenomic sequencing randomly fragments and sequences all DNA present within a sample (Laudadio et al., 2018). This approach simultaneously identifies microbial taxa and the functional genes they harbour, providing insights into both community composition and metabolic potential.

One of the major strengths of metagenomics is its ability to generate taxonomic and functional information within a single analysis (Bağcı et al., 2019). Microbial communities that differ considerably in taxonomic composition may nevertheless possess similar functional capabilities because key nutrient cycling genes are often shared among phylogenetically distinct microorganisms (Castellano-Hinojosa & Strauss, 2021). Consequently, gene centric metagenomic analyses frequently provide a more meaningful assessment of ecosystem functioning than taxonomy-based approaches alone. Recent advances in genome resolved metagenomics have further strengthened this capability by assembling sequencing reads into metagenome-assembled genomes (MAGs), thereby enabling functional genes involved in processes such as nitrification, phosphorus acquisition and carbon metabolism to be assigned to specific microbial genomes (Mirete et al., 2025). This genome level resolution has considerably improved our understanding of the ecological roles performed by individual microorganisms within highly complex soil communities.

3.2 Insights from Soil Metagenomics for Sustainable Agriculture

The application of metagenomics has substantially advanced our understanding of the genetic mechanisms that underpin soil biogeochemical processes essential for sustainable agriculture. By identifying functional genes involved in nutrient cycling, metagenomics has provided valuable insights into the microbial processes regulating soil fertility and crop productivity (Jia et al., 2025).

Large-scale metagenomic investigations have identified diverse functional genes associated with nitrogen cycling, including those involved in biological nitrogen fixation (nifH), ammonia oxidation (amoA), nitrite oxidation (nxrA) and the multiple pathways of nitrate reduction and denitrification (Wang et al., 2022). Similarly, genes associated with phosphorus acquisition, including phosphate-starvation regulators, phosphate-solubilization genes (gcd),

phosphatases (phoD) and phosphate transport systems, have been widely characterized across agricultural soils (Siles et al., 2022).

Importantly, the abundance and diversity of these functional genes respond consistently to agricultural management practices such as fertilizer application, cropping systems, vegetation type and soil physicochemical properties, particularly soil pH (Li et al., 2020). Consequently, metagenomic analyses provide early molecular indicators of changes in nutrient cycling potential that often precede measurable responses in crop growth and yield (Berg et al., 2020).

Comparative metagenomic studies have also demonstrated that microbial taxonomy and functional capacity are not always closely linked. Functional genes responsible for essential processes such as nitrification and phosphorus solubilization are frequently distributed among taxonomically diverse microorganisms, resulting in considerable functional redundancy (Louca et al., 2018). As a result, substantial changes in microbial community composition may occur without corresponding losses in ecosystem functioning. These findings reinforce the importance of evaluating functional gene profiles in addition to microbial taxonomic composition when assessing soil health and ecosystem resilience.

3.3 From Genetic Potential to Functional Activity

Despite its considerable strengths, metagenomics primarily reveals the genetic potential encoded within microbial genomes rather than the biological processes that are actively occurring at the time of sampling (Pérez-Cobas et al., 2020). The presence of genes associated with nutrient cycling does not necessarily indicate that these genes are being transcribed, translated or contributing to ecosystem functioning under prevailing environmental conditions (Preheim et al., 2025). For example, microorganisms may possess phosphate-solubilizing genes, yet these genes remain inactive unless triggered by specific nutrient limitations or environmental cues (Pang et al., 2024).

This distinction between genetic potential and functional activity represents one of the principal limitations of metagenomics in agricultural research. Agricultural management practices, including fertilizer application, biofertilizer inoculation and soil amendments, can induce substantial changes in microbial metabolism without markedly altering the abundance of functional genes (Shittu et al., 2026). Consequently, metagenomic analyses alone may overlook important physiological responses that directly influence nutrient availability, plant performance and overall soil functioning (Leite et al., 2022). Addressing this limitation requires complementary approaches capable of measuring gene expression, protein synthesis and metabolite production (Moshood et al., 2025).

Functional multi-omics including metatranscriptomics, metaproteomics and metabolomics bridges this gap by revealing not only the genetic capabilities of soil microbial communities but also the biological functions they actively perform under specific environmental conditions (Li et al., 2026). By linking microbial genetic potential with realized biological activity, these integrated approaches bridge microbial community composition with ecosystem function, providing a systems-level understanding of soil microbial ecology.

4. Functional Multi-Omics: From Genetic Potential to Realized Function

The limitations of metagenomics in distinguishing between microbial genetic potential and actual biological activity have driven the development of functional multi-omics. While metagenomics provides valuable information about the genes present within microbial communities, understanding how these genes are regulated, translated and ultimately expressed as biological functions requires additional molecular layers of analysis (Roller et al., 2013). Functional multi-omics addresses this need by integrating metatranscriptomics, metaproteomics and metabolomics into a unified systems biology framework, thereby providing a comprehensive understanding of microbial functioning from genotype to phenotype (Aguiar-Pulido et al., 2016).

Unlike individual omics approaches, which capture only a single aspect of microbial activity, functional multi-omics simultaneously investigates gene expression, protein synthesis and metabolite production, enabling researchers to trace the complete molecular pathway from microbial genetic potential to realized biological function (Sahoo et al., 2021). Because each omics layer reflects a different stage of cellular regulation and possesses distinct methodological strengths and limitations, their integration offers a far more accurate representation of microbial processes than any single technique alone (Yan et al., 2026). Consequently, functional multi-omics has become an increasingly valuable approach for understanding how soil microorganisms respond to changing environmental conditions and agricultural management practices, thereby supporting the development of more sustainable and resilient agricultural systems.

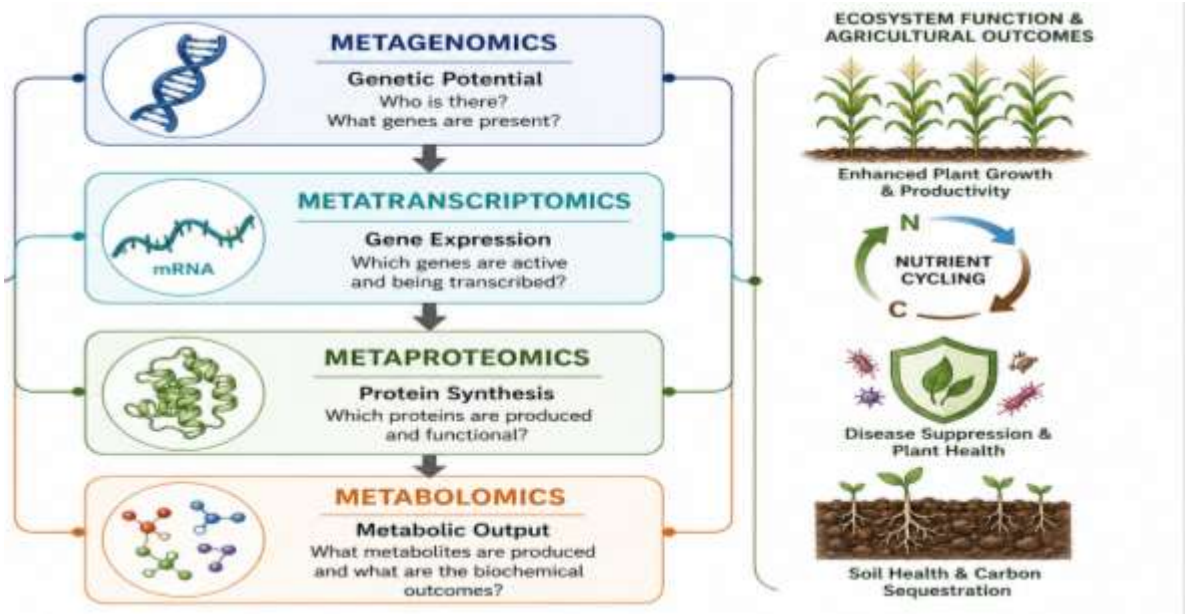

Figure 1. Integrated functional multi-omics workflow connecting soil microbial genetic potential to agricultural ecosystem services.

4.1 Metatranscriptomics: Revealing Active Gene Expression

Among the different functional omics approaches, metatranscriptomics provides the first indication of microbial activity by identifying genes that are actively being transcribed. Because messenger RNA (mRNA) reflects the immediate physiological response of microorganisms to environmental stimuli, metatranscriptomics offers a real time snapshot of microbial function under prevailing soil conditions (Mukherjee & Reddy, 2020).

Metatranscriptomics investigates the actively transcribed messenger RNA (mRNA) within microbial communities, providing insights into gene expression under specific environmental conditions. (Tyagi & Katara, 2024). Unlike DNA, which represents relatively stable genetic information, mRNA has a short half-life, allowing researchers to capture rapid microbial responses to drought stress, nutrient availability, pathogen invasion and fluctuations in root exudation (Falk et al., 2025). Consequently, metatranscriptomics reveals not only the functional capacity of soil microorganisms but also the biological processes that are actively occurring at the time of sampling.

A major advantage of metatranscriptomics lies in its integration with metagenomic datasets (Morales & Holben, 2011). By mapping RNA sequences onto assembled metagenomes or metagenome-assembled genomes (MAGs), researchers can determine which microorganisms are actively contributing to specific ecosystem processes. This integrated approach frequently demonstrates that microorganisms present at relatively low abundance can exhibit disproportionately high metabolic activity, highlighting that ecological importance is not always reflected by numerical abundance (Yang et al., 2026). Such findings considerably enhance our understanding of the functional dynamics governing complex soil microbial communities.

4.2 Metaproteomics: Confirming Functional Activity

Although transcription provides valuable evidence of microbial responses, gene expression alone does not necessarily predict protein production. Transcription, translation and post-translational regulation are independently controlled processes, meaning that transcript abundance does not always correspond to functional enzyme activity (Liu et al., 2016). Consequently, direct analysis of proteins is essential for confirming whether expressed genes ultimately contribute to biological processes within the soil ecosystem (Starke et al., 2019). Metaproteomics addresses this limitation by directly identifying and quantifying proteins produced by the entire microbial community using high resolution mass spectrometry (Pan et al., 2024). Because proteins are the primary functional molecules responsible for catalysing biochemical reactions, metaproteomics provides direct evidence of microbial activity within the soil environment (Starke et al., 2019).

Beyond protein identification, metaproteomics also provides valuable information on post-translational modifications, enzyme activation and protein-protein interactions that cannot be detected through transcriptomic analyses alone (Shrestha et al., 2021). Nevertheless, applying metaproteomics to soil remains technically challenging because soil is an exceptionally complex matrix containing extracellular proteins, intracellular proteins, humic substances and mineral particles that interfere with protein extraction and identification (Pan et al., 2024). Furthermore, incomplete reference databases and the immense taxonomic diversity of soil microorganisms frequently complicate peptide annotation, particularly for previously undescribed microbial taxa.

4.3 Metabolomics: Measuring the Chemical Outcome

While metatranscriptomics identifies active gene expression and metaproteomics confirms protein production, metabolomics captures the final biochemical outcome of microbial activity. Because metabolites represent the end products of cellular metabolism, they provide the closest molecular representation of the physiological status of the plant-soil system (Brown et al., 2024). Metabolomics characterizes the complete repertoire of low molecular weight

metabolites present within the soil-plant environment (Feussner & Polle, 2015). Using analytical platforms such as mass spectrometry and nuclear magnetic resonance spectroscopy, it identifies diverse compounds including organic acids, amino acids, sugars, phytohormones and secondary metabolites produced by both plants and microorganisms (Vinay et al., 2021).

Consequently, metabolomics provides direct evidence of the biochemical processes occurring within the soil ecosystem. Metabolomic analyses have substantially advanced our understanding of rhizosphere interactions by identifying chemical signals involved in plant-microbe communication, microbial recruitment, nutrient mobilization and stress adaptation (Sibanyoni et al., 2025). Changes in metabolite profiles often precede detectable shifts in microbial community composition, making metabolomics particularly valuable for evaluating the functional consequences of agricultural management practices and environmental change (Withers et al., 2020).

4.4 Integrating Multi-Omics for Sustainable Agriculture

Although each omics approach provides valuable information individually, their greatest strength lies in their integration. Combining metagenomics, metatranscriptomics, metaproteomics and metabolomics enables researchers to connect microbial identity with gene expression, protein synthesis and metabolic activity thereby, providing a holistic understanding of soil ecosystem functioning (Aguiar-Pulido et al., 2016).

Recent advances in systems biology have facilitated the integration of these datasets through correlation network analysis, genome-scale metabolic modelling and machine learning based analytical frameworks (Sanches et al., 2024). These approaches establish direct links between microbial community composition, transcriptional activity, protein production and metabolite synthesis allowing complex biological interactions to be interpreted at a systems level (Parveen et al., 2026). However, cross ecosystem investigations have demonstrated that relationships among microbial taxa, functional genes, proteins and metabolites vary considerably across different environments, indicating that analytical frameworks developed for one ecosystem cannot always be directly transferred to agricultural soils (Hicks et al., 2022). This highlights the need for soil specific multi-omics integration strategies capable of accurately capturing the complexity of agricultural ecosystems.

For sustainable agriculture, integrated functional multi-omics transforms microbial profiling from a descriptive inventory into a predictive and actionable framework. For example, a soil may exhibit an apparently stable metagenomic inventory of nitrogen fixation genes while simultaneously displaying reduced transcription of those genes, diminished nitrogenase protein abundance and lower concentrations of nitrogen-related metabolites (Sun et al., 2021). Such integrated evidence indicates that nitrogen fixation is functionally impaired despite the underlying genetic potential remaining intact, thereby guiding management interventions such as pH adjustment, improved soil aeration or optimized fertilizer application (Dong et al., 2024). By bridging the gap between microbial potential and realized ecosystem function, functional multi-omics provides a powerful framework for understanding soil health and developing precision management strategies that enhance agricultural sustainability.

5. The Plant–Soil–Microbiome Interface: Mechanistic Insights

The application of functional multi-omics has significantly advanced our understanding of the complex interactions occurring at the plant–soil–microbiome interface. Rather than functioning as independent biological entities, plants, soil and microorganisms form an integrated and dynamic system in which continuous molecular communication regulates nutrient cycling, plant health, stress adaptation and overall ecosystem functioning (Bhimani et al., 2024). By integrating multiple layers of molecular information, functional multi-omics has revealed not only the composition of microbial communities but also the mechanisms through which plants and microorganisms influence one another, providing unprecedented insights into the biological processes that sustain agricultural productivity (Suresh et al., 2025).

5.1 The Rhizosphere and Root Exudates

At the centre of these interactions lies the rhizosphere, the narrow zone of soil directly influenced by root growth and activity, where intense biological, chemical and physical processes occur (Slaughter, 2021). Plants allocate a substantial proportion of their photosynthetically fixed carbon to this region through the release of root exudates, creating a nutrient rich environment that supports highly diverse microbial communities. These exudates comprise a complex mixture of organic acids, sugars, amino acids, phytohormones, vitamins, phenolic compounds, flavonoids, terpenoids and other secondary metabolites that function not only as carbon and energy sources but also as signaling molecules regulating plant-microbe interactions (Wankhade et al., 2025).

Root exudates play a central role in shaping rhizosphere microbial communities by selectively recruiting beneficial microorganisms while simultaneously influencing microbial activity and community assembly (Zhalnina et al., 2018). Microorganisms detect these chemical gradients through specialized sensory systems, including methyl-accepting chemotaxis proteins, enabling motile bacteria to migrate towards actively growing roots (O'Neal et al., 2020). Importantly, root exudation is not merely a passive consequence of plant metabolism but a highly regulated process that varies according to plant developmental stage, nutrient availability and environmental stress (Robert et al., 2025).

For example, under nitrogen deficient conditions, legumes increase the secretion of flavonoids that selectively attract compatible rhizobia, thereby facilitating biological nitrogen fixation (Liu & Murray, 2016). Recent advances in metabolomics have greatly enhanced understanding of these interactions by identifying individual exudate compounds and elucidating their specific roles in microbial recruitment and rhizosphere assembly (Suresh et al., 2025). These findings demonstrate that the rhizosphere is not simply a zone of microbial colonization but a

chemically regulated environment in which plants actively shape the composition and function of their associated microbiome.

5.2 Molecular Dialogues and Beneficial Outcomes

Following microbial recruitment, successful colonization depends on an intricate molecular dialogue between plants and microorganisms. Plants initially recognize conserved microbial molecules, known as microbe associated molecular patterns (MAMPs), through pattern recognition receptors located on the root surface, thereby activating pattern triggered immunity (PTI), which constitutes the first line of defence against microbial invasion (Yu et al., 2017). However, because beneficial microorganisms often possess many of the same conserved molecular signatures as pathogens, they must carefully modulate host immune responses to establish stable and mutually beneficial associations (Yu et al., 2019).

Plant growth-promoting rhizobacteria (PGPR) achieve this by producing a diverse range of metabolites and enzymes that regulate plant hormonal signalling pathways (Irfan et al., 2026). For instance, bacterial ACC deaminase lowers stress-induced ethylene accumulation, thereby alleviating the inhibition of root growth and facilitating successful microbial colonization (Etesami et al., 2020). Likewise, beneficial microorganisms influence jasmonic acid, ethylene and salicylic acid mediated signalling pathways resulting in induced systemic resistance (ISR), a primed physiological state that enhances the plant's capacity to withstand subsequent pathogen attack (Yu et al., 2022). Through these coordinated molecular interactions, microorganisms improve nutrient acquisition, stimulate root development, enhance tolerance to abiotic stresses such as drought and salinity, suppress soil-borne pathogens and ultimately increase plant growth and productivity (Dhiman et al., 2026).

Functional multi-omics has substantially strengthened the mechanistic understanding of these processes by integrating complementary layers of molecular information. While metagenomics identifies the microorganisms and functional genes present within the rhizosphere, metatranscriptomics reveals the genes actively expressed during plant-microbe interactions, metaproteomics confirms the proteins responsible for these biological functions and metabolomics identifies the signaling molecules exchanged between plants and microorganisms (Srivastava & Sarethy, 2021). Collectively, these complementary approaches provide a systems level understanding of the plant-soil-microbiome interface, demonstrating how molecular communication governs microbial community assembly, regulates ecosystem processes and supports sustainable agricultural productivity.

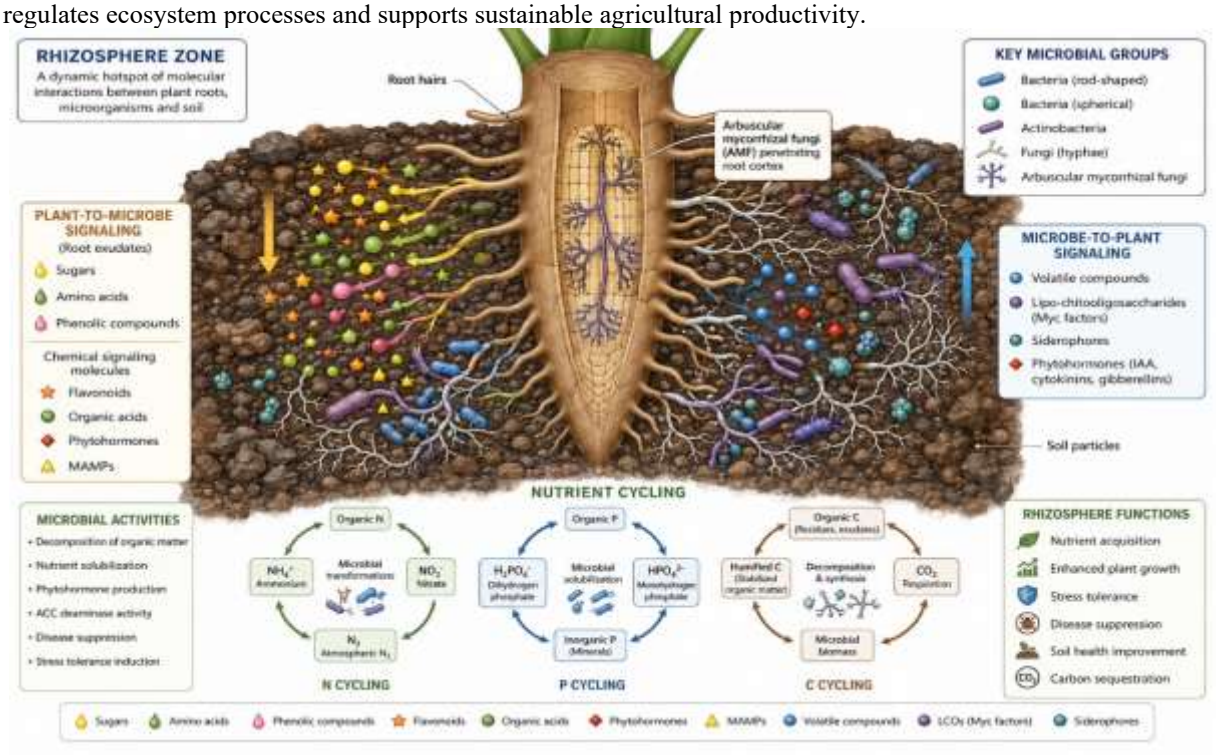

Figure 2. Molecular dialogues and functional outcomes at the plant-soil-microbiome interface

6. Functional Multi-Omics Discoveries with Direct Relevance to Sustainable Agriculture

The integration of metagenomics, metatranscriptomics, metaproteomics and metabolomics has transformed soil microbiology from descriptive community profiling to a mechanistic understanding of microbial functioning. By linking microbial identity with gene expression, protein synthesis and metabolite production, functional multi-omics has revealed the molecular mechanisms underlying nutrient cycling, disease suppression, abiotic stress tolerance and carbon sequestration (Li et al., 2026). These advances have substantially expanded understanding of how soil microorganisms influence agricultural productivity and sustainability, while providing new opportunities to improve nutrient-use efficiency, enhance crop resilience, reduce chemical inputs and promote long-term soil health (Pandey & Saharan, 2025).

6.1 Functional Regulation of Nitrogen and Phosphorus Cycling

Among the various ecosystem services provided by soil microorganisms, nutrient cycling remains one of the most fundamental determinants of agricultural productivity. Nitrogen and phosphorus are the primary nutrients limiting crop growth and their transformation within the soil is largely regulated by microbial activity (Bayu, 2024). Although metagenomics has successfully identified numerous functional genes associated with these processes, functional multi-omics has demonstrated that the presence of these genes alone does not necessarily reflect their biological activity (Wani et al., 2025).

Metatranscriptomic analyses have revealed that genes involved in nitrogen fixation, nitrification, denitrification, phosphate solubilization and phosphorus mineralization are differentially expressed under varying fertilization regimes, enabling researchers to distinguish between soils that merely possess nutrient cycling potential and those actively performing these functions (Du et al., 2023). These findings emphasize that microbial activity is highly dynamic and responds directly to agricultural management and environmental conditions.

Similarly, comparative studies across different land use systems and plantation types have demonstrated that microbial phosphorus cycling pathways respond rapidly to nutrient availability (Martins et al., 2026). Under phosphorus deficient conditions, microorganisms increase the expression of genes involved in phosphate solubilization and mineralization as an adaptive strategy to enhance phosphorus acquisition (Wu et al., 2022). Such mechanistic insights provide valuable molecular evidence for optimizing fertilizer management and support the development of low input, resource efficient agricultural systems that capitalize on indigenous microbial functions.

6.2 Understanding Disease Suppressive Soils

Beyond nutrient acquisition, functional multi-omics has substantially improved our understanding of the microbial mechanisms that protect plants against disease. Disease suppressive soils represent one of the clearest examples of how microbial community function directly influences plant health. In these soils, soil-borne pathogens either fail to establish, cause only limited disease or progressively lose their capacity to induce infection (Latz et al., 2016). This suppression results from three complementary mechanisms, general suppression through intense microbial competition, specific suppression mediated by antagonistic microorganisms and induced suppression, whereby the microbial community reorganizes in response to pathogen invasion (Schlatter et al., 2017).

Functional multi-omics has played a pivotal role in elucidating the molecular basis of these suppressive mechanisms. Functional amplicon sequencing targeting non-ribosomal peptide synthetase (NRPS) genes has identified microbial biosynthetic pathways responsible for producing antifungal secondary metabolites that distinguish Fusarium suppressive soils from disease conducive soils (Tracanna et al., 2021). Earlier studies integrating PhyloChip analysis with metagenomics similarly identified bacterial consortia responsible for suppressing Rhizoctonia solani in sugar beet rhizospheres, thereby establishing the foundation for subsequent transcriptomic and metabolomic investigations (Wolfgang et al., 2020).

Recent metabolomic studies have further demonstrated that plants actively participate in disease suppression through the "cry for help" mechanism (Rizaludin et al., 2021). Under pathogen attack or environmental stress, plants modify the composition of their root exudates to selectively recruit beneficial microorganisms capable of suppressing pathogens while simultaneously enhancing host defence responses (Spooren et al., 2024). This phenomenon provides a direct mechanistic link between the molecular interactions occurring within the rhizosphere and practical disease management strategies for sustainable agriculture.

6.3 Enhancing Drought and Salinity Tolerance

As climate change intensifies the frequency and severity of drought and salinity, understanding microbial mechanisms that enhance plant resilience has become increasingly important. Functional multi-omics has revealed that beneficial microorganisms improve stress tolerance through coordinated regulation of plant hormonal signalling, osmotic adjustment, antioxidant defence and root system architecture (Chakrovarty et al., 2026).

Integrated transcriptomic, proteomic and metabolomic investigations consistently demonstrate that plant growth-promoting microorganisms regulate key hormonal pathways involving abscisic acid (ABA), ethylene, jasmonic acid, salicylic acid and auxins (Song et al., 2026). Beneficial bacteria producing ACC deaminase reduce stress-induced ethylene accumulation, while microbial synthesis of exopolysaccharides and compatible solutes enhances cellular water retention and protects plants against osmotic stress (Singh et al., 2022). Simultaneously, microbial interactions stimulate modifications in root architecture that improve water and nutrient acquisition under adverse environmental conditions.

A representative example is provided by the inoculation of maize with the diazotrophic bacteria Azospirillum brasilense and Herbaspirillum seropedicae, where integrated transcriptomic and physiological analyses demonstrated reduced expression of a maize ABA biosynthesis gene (Irineu et al., 2022). This modulation alleviated drought induced hormonal imbalance and significantly improved plant adaptation to water deficit (Upadhyay et al., 2022). Such findings illustrate how functional multi-omics can identify the precise molecular mechanisms through which beneficial microorganisms enhance crop resilience under environmental stress.

6.4 Carbon Sequestration and Microbial Necromass Formation

In addition to supporting crop productivity, soil microorganisms play a fundamental role in long term carbon sequestration and climate regulation. Recent multi-omics investigations have substantially revised the traditional understanding of soil organic carbon formation (Overy et al., 2021). Rather than originating predominantly from chemically recalcitrant plant residues, a significant proportion of stable soil organic carbon is now recognized to derive from microbial necromass, the residual cellular material and extracellular compounds remaining after

microbial death (Rempfert et al., 2024). This emerging paradigm highlights microbial carbon use efficiency, microbial turnover and mineral stabilization of necromass as the principal biological drivers of long-term carbon storage.

Functional multi-omics has further demonstrated that microbial death pathways, including starvation, predation and viral lysis, not only influence the quantity of necromass produced but also determine its biochemical composition and subsequent stabilization within soil aggregates (Etesami, 2026). Consequently, microbial necromass formation is increasingly recognized as a biologically regulated process that can be investigated at genomic, proteomic and metabolomic levels (Wu et al., 2023).

Importantly, these mechanistic insights have direct implications for agricultural management. A global meta-analysis comprising 481 paired field observations demonstrated that conservation practices such as reduced or no tillage, organic manure application and straw incorporation increased cropland microbial necromass carbon by approximately 12–21%, with the greatest improvements occurring when these practices were implemented in combination (Zhou et al., 2023). These findings provide compelling evidence that management practices promoting microbial activity and necromass accumulation can simultaneously improve soil fertility, enhance carbon sequestration and strengthen climate-smart agricultural systems.

7. Translating Functional Multi-Omics Insights into Sustainable Agricultural Practice

The mechanistic understanding generated through functional multi-omics is increasingly being translated into practical agricultural innovations. By identifying key microbial taxa, functional genes, metabolic pathways and plant-microbe interactions, multi-omics provides the scientific foundation for developing targeted microbiome based strategies that improve crop productivity while reducing environmental impacts (Diwan et al., 2022). These advances are reshaping modern agriculture through microbiome engineering, microbiome informed crop breeding and the development of biologically based alternatives to conventional agrochemicals, thereby supporting more resilient, resource efficient and climate-smart farming systems.

7.1 Microbiome Engineering: Designing Synthetic Microbial Communities

One of the most promising applications of functional multi-omics is the rational design of microbial communities capable of performing multiple beneficial functions simultaneously. Conventional microbial inoculants generally consist of single microbial strains selected for specific plant growth-promoting characteristics (Zaramela et al., 2021). Although these inoculants often perform well under controlled laboratory or greenhouse conditions, their effectiveness under field conditions is frequently inconsistent because introduced microorganisms must compete with well established native microbial communities and often lack the functional diversity required to support plants under fluctuating environmental conditions (Sarker et al., 2026).

To overcome these limitations, synthetic microbial communities (SynComs) have emerged as an innovative microbiome engineering strategy. SynComs are deliberately assembled microbial consortia composed of taxonomically and functionally complementary microorganisms selected to collectively perform multiple ecological functions, including nutrient acquisition, disease suppression, stress tolerance and efficient rhizosphere colonization (Zhang et al., 2026). The design of these microbial consortia increasingly relies on functional multi-omics, which enables researchers to identify keystone taxa, complementary metabolic pathways and ecological interactions that promote stable community establishment and enhanced plant performance (Xu et al., 2026).

The practical value of this approach has recently been demonstrated in maize, where a teosinte derived seven strain SynCom was evaluated alongside conventional urea fertilization and drone assisted phosphorus application. Integrated multi-omics analyses revealed significant changes in bacterial and fungal community composition that were accompanied by measurable improvements in soil functionality and crop performance (Hernández-García et al., 2025). This study illustrates how microbiome engineering, precision agriculture and advanced molecular technologies are beginning to converge to develop more efficient and sustainable crop management strategies.

7.2 Microbiome-Informed Crop Breeding

In addition to engineering microbial communities, functional multi-omics has demonstrated that plants themselves play an active role in shaping their associated microbiome. Plant genotype significantly influences the composition and functional characteristics of rhizosphere microbial communities, leading to the recognition that microbiome recruitment is, at least in part, a heritable trait (Negre Rodríguez et al., 2025).

Genome wide association studies have identified host genetic loci associated with the recruitment of beneficial microbial taxa (Deng et al., 2021), while comparative studies of crop domestication suggest that historical breeding has inadvertently selected for microbial communities capable of enhancing nutrient acquisition, plant growth and stress resilience (Ramirez-Villacis et al., 2025). These findings have given rise to the concept of microbiome informed breeding, in which crop improvement programmes aim not only to optimize plant genetics but also to enhance the recruitment and maintenance of beneficial microbial communities (Kumar et al., 2026).

Nevertheless, translating this concept into routine breeding programmes remains challenging because the composition and function of rhizosphere microbial communities are strongly influenced by environmental conditions, soil properties and plant developmental stage. Consequently, microbiome heritability often varies across different production systems (Araujo et al., 2025). To address this challenge, some researchers advocate selecting plant phenotypes associated with beneficial microbiome recruitment rather than relying exclusively on host genotype, thereby integrating plant performance with microbiome functionality during crop improvement (Song et al., 2020).

7.3 Reducing Chemical Inputs through Microbial Biofertilizers

The mechanistic insights generated through functional multi-omics also provide strong scientific support for reducing dependence on synthetic fertilizers and pesticides. The molecular processes including biological nitrogen fixation, phosphate solubilization, induced systemic resistance, phytohormone regulation and microbial enhancement of abiotic stress tolerance, collectively demonstrate the capacity of beneficial microorganisms to function as sustainable alternatives to conventional agrochemicals.

Functional multi-omics has facilitated the identification of microbial strains possessing complementary plant growth-promoting characteristics while simultaneously revealing the molecular mechanisms responsible for their beneficial effects (Sahoo et al., 2025). These insights have accelerated the development of more effective biofertilizers and microbial formulations tailored to specific crops, soils and environmental conditions. Consequently, microbiome based products are increasingly being incorporated into integrated nutrient management strategies to improve nutrient-use efficiency, enhance crop resilience and reduce the environmental impacts associated with intensive fertilizer use (Singh et al., 2025).

Despite these advances, achieving consistent field performance remains a major challenge. The effectiveness of microbial inoculants depends not only on microbial functionality but also on formulation quality, carrier compatibility, shelf life, survival during storage and successful establishment within native soil microbial communities (Lobo et al., 2019). Addressing these formulation and delivery constraints therefore remains essential for translating laboratory discoveries into reliable agricultural technologies that can be adopted on a large scale (Fadiji et al., 2024).

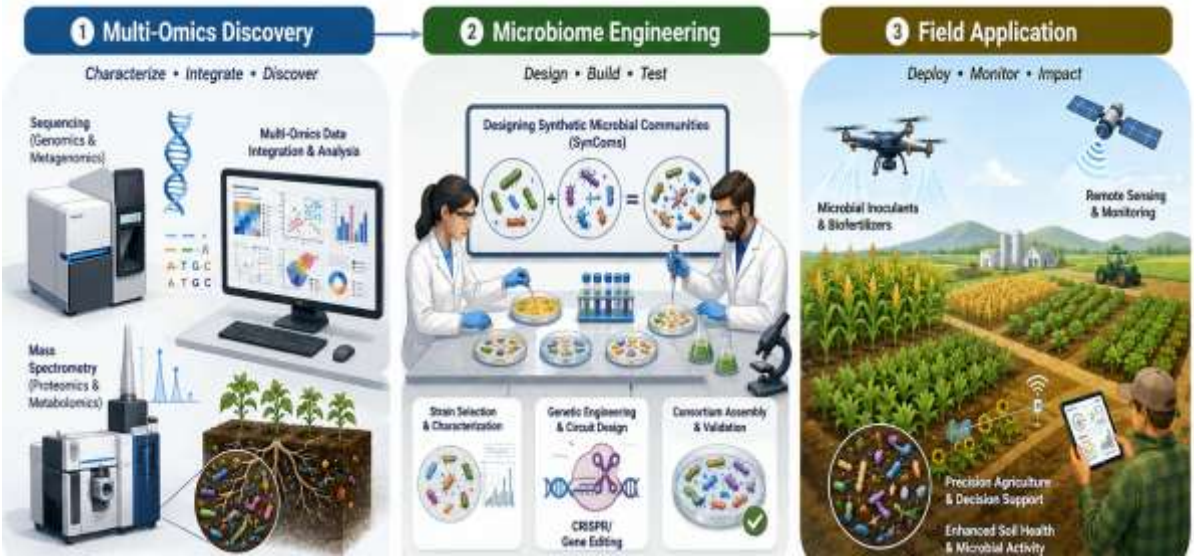

Figure 3. The translational pipeline from multi-omics discovery to field-scale sustainable agriculture.

8. Challenges and Future Perspectives

Despite the remarkable advances achieved through functional multi-omics, several scientific, technical, computational and practical challenges continue to limit its widespread application in sustainable agriculture. Although integrated multi-omics has substantially improved mechanistic understanding of plant-soil-microbiome interactions, translating these discoveries into reliable field scale technologies remains a major challenge. Addressing these limitations will be essential for harnessing the full potential of functional multi-omics to improve crop productivity, soil health and environmental sustainability.

From a technical perspective, the absence of standardized protocols for sample collection, nucleic acid extraction, protein isolation, metabolite analysis, sequencing and data processing remains a significant obstacle (Ece et al., 2026). Variations in experimental methodologies among laboratories often reduce the reproducibility of multi-omics datasets and hinder direct comparisons across independent studies (Tarazona et al., 2020). Furthermore, reference databases remain incomplete for many taxonomically novel and uncultured soil microorganisms, making accurate functional annotation and taxonomic assignment particularly challenging (Keck et al., 2023). Another important limitation is the disparity between controlled experimental environments and agricultural field conditions, where microbial interactions are influenced by highly heterogeneous soil properties, climatic variability and management practices. Consequently, microbial functions identified under greenhouse conditions frequently fail to perform consistently under field conditions (Dao & Ho, 2026).

Beyond experimental challenges, the integration of multiple omics datasets presents substantial computational difficulties. Combining metagenomic, metatranscriptomic, metaproteomic and metabolomic datasets into a unified biological framework requires sophisticated computational tools capable of integrating highly heterogeneous data types (Pedersen et al., 2018). Although numerous statistical, systems biology and machine learning approaches have been developed, standardized analytical workflows remain limited, making comparisons across studies difficult (Fernandes & Husi, 2019). Moreover, most current multi-omics investigations primarily identify statistical

associations between microbial taxa, functional genes, metabolites and plant traits rather than establishing direct causal relationships. Demonstrating causality therefore requires complementary experimental validation using synthetic microbial communities or targeted functional assays (Chesneau et al., 2025).

Another major challenge lies in capturing the spatial and temporal complexity of agricultural soils. Most multi-omics investigations rely on single sampling events conducted at relatively few locations, providing only static representations of highly dynamic soil ecosystems (Joos et al., 2025). However, rhizosphere microbial communities continuously change throughout plant development and respond to variations in soil depth, environmental conditions and agricultural management practices. Understanding these dynamic interactions will therefore require long term, high resolution investigations capable of monitoring microbial community structure and function across multiple growing seasons and diverse agroecosystems (Shah et al., 2025).

In addition to scientific and technical limitations, regulatory and biosafety considerations remain critical for the successful implementation of microbiome based technologies. Existing regulatory frameworks were primarily designed for chemical fertilizers and pesticides and are often inadequate for evaluating living microbial products (Köhl, 2025). Consequently, inconsistencies persist in the classification and regulation of products marketed as biofertilizers, biostimulants or biologicals (Sible et al., 2025). Furthermore, the deliberate introduction of non-native or engineered microorganisms into agricultural ecosystems raises important concerns regarding ecological safety, persistence, horizontal gene transfer and long-term impacts on native microbial communities (Mawarda et al., 2020). Developing harmonized regulatory frameworks together with comprehensive biosafety assessments will therefore be essential for the responsible deployment of microbiome-based agricultural innovations.

Despite these challenges, the future of functional multi-omics in agriculture remains highly promising. One of the most significant emerging directions is the transition towards site-specific microbiome management, where integrated multi-omics profiling is used to characterize the microbial and functional status of individual fields and guide customized recommendations for microbial inoculants, nutrient amendments, crop rotations and soil management practices rather than relying on generalized management strategies (Li et al., 2026). At the same time, integrating host genetics with microbiome engineering is expected to accelerate microbiome-informed breeding programmes capable of simultaneously optimizing crop genotypes and their associated beneficial microbial communities, thereby improving nutrient-use efficiency, disease resistance and climate resilience (Escudero-Martinez & Bulgarelli, 2023).

Looking further ahead, future research should increasingly focus on understanding how microbial communities respond to multiple interacting environmental stresses, including drought, salinity, heat, flooding, nutrient limitation and pathogen pressure (Fernández-Triana et al., 2024). Functional multi-omics provides an ideal platform for investigating these complex responses because it captures microbial activity across multiple molecular levels, from genetic potential to metabolic function (Chetty & Blekhman, 2024). The continued integration of multi-omics with artificial intelligence, precision agriculture, remote sensing, digital agriculture and predictive ecological modelling is expected to transform microbiome research into a predictive and decision-support framework capable of guiding climate-smart agricultural management.

Overall, continued advances in experimental standardization, computational integration, field validation and regulatory harmonization will be instrumental in transforming functional multi-omics from a predominantly research oriented approach into a practical agricultural technology (Hemme et al., 2026). Achieving this transition will enable microbiome research to move beyond descriptive analyses towards predictive and actionable solutions that improve crop productivity, maintain soil health and promote long term agricultural sustainability.

9. CONCLUSION

Functional multi-omics has fundamentally transformed our understanding of soil microbiomes by shifting the focus from describing microbial diversity to elucidating the molecular mechanisms that regulate ecosystem functioning (Li et al., 2026). While metagenomics provides valuable insights into the genetic potential of microbial communities, its integration with metatranscriptomics, metaproteomics and metabolomics enables a comprehensive understanding of how microbial genes are expressed, translated into functional proteins and ultimately manifested as metabolic activities under specific environmental conditions (Aguiar-Pulido et al., 2016). This systems level perspective has significantly advanced our understanding of the intricate interactions occurring at the plant-soil-microbiome interface and their contribution to sustainable agricultural productivity.

The integration of multiple omics approaches has revealed the indispensable roles of soil microorganisms in regulating nutrient cycling, suppressing plant diseases, enhancing tolerance to abiotic stresses and promoting long term carbon sequestration (Parveen et al., 2026). By linking microbial identity with functional activity, multi-omics has transformed microbiome research from predominantly descriptive ecological investigations into mechanistic studies with direct agricultural relevance (Roy et al., 2026). These advances have facilitated the identification of functional microbial consortia, key signalling pathways and metabolite-mediated plant-microbe interactions, thereby creating new opportunities for microbiome engineering, microbiome informed crop breeding and the development of next generation biofertilizers capable of reducing dependence on synthetic agrochemicals while improving crop productivity and soil health (De Souza et al., 2020).

Despite these remarkable advances, several challenges must be addressed before functional multi-omics can be routinely implemented in agricultural practice. Standardized experimental protocols, robust computational frameworks for multi-omics data integration, comprehensive reference databases, long term field validation and

harmonized regulatory policies remain essential for translating laboratory discoveries into reliable field applications (Syeda, 2025). Furthermore, integrating functional multi-omics with emerging technologies such as artificial intelligence, precision agriculture, remote sensing, digital agriculture and predictive ecological modelling is expected to accelerate the development of data driven management strategies capable of addressing increasingly complex agricultural and environmental challenges (Liang et al., 2025).

Overall, functional multi-omics represents a transformative framework for advancing sustainable agriculture by bridging microbial diversity with ecosystem function and agronomic performance. As technological innovations continue to improve analytical resolution, computational integration and systems level interpretation, multi-omics will play an increasingly central role in designing resilient, climate smart agricultural systems that optimize nutrient-use efficiency, strengthen plant health, enhance soil carbon storage and promote long term food security and environmental sustainability. By integrating molecular scale insights with practical field applications, functional multi-omics has the potential to redefine future agricultural management and support the transition towards more productive, resource efficient and environmentally sustainable farming systems.

CONFLICT OF INTEREST

The authors declare that they have no financial or personal relationships that could be construed as a potential conflict of interest with respect to the research and content presented in this review article. No funding was received for the preparation of this review and the authors have no affiliations with organizations or entities that could influence the objectivity of the review. All sources and data included have been selected and analysed impartially. Any potential biases have been disclosed and efforts have been made to provide a comprehensive and balanced perspective on the subject matter.

Author's declaration

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

REFERENCE

1. Aguiar-Pulido, V., Huang, W., Suarez-Ulloa, V., Cickovski, T., Mathee, K., & Narasimhan, G. (2016). Metagenomics, metatranscriptomics, and metabolomics approaches for microbiome analysis: supplementary issue: bioinformatics methods and applications for big metagenomics data. Evolutionary bioinformatics, 12, EBO-S36436. https://doi.org/10.4137/EBO.S36436
2. Araujo, A. S., Pereira, A. P., de Medeiros, E. V., & Mendes, L. W. (2025). Root architecture and the rhizosphere microbiome: shaping sustainable agriculture. Plant Science, 359, 112599. https://doi.org/10.1016/j.plantsci.2025.112599
3. Bağcı, C., Beier, S., Górska, A., & Huson, D. H. (2019). Introduction to the analysis of environmental sequences: metagenomics with MEGAN. In Evolutionary genomics: statistical and computational methods (pp. 591-604). New York, NY: Springer New York. https://doi.org/10.1007/978-1-4939-9074-0_19
4. Bahram, M., Hildebrand, F., Forslund, S. K., Anderson, J. L., Soudzilovskaia, N. A., Bodegom, P. M., ... & Tedersoo, L. (2018). Structure and function of the global topsoil microbiome. Nature, 560(7717), 233–237. https://doi.org/10.1038/s41586-018-0386-6
5. Bayu, T. (2024). Systematic review on the role of microbial activities on nutrient cycling and transformation implication for soil fertility and crop productivity. bioRxiv, 2024-09. https://doi.org/10.1101/2024.09.02.610905
6. Berg, G., Rybakova, D., Fischer, D., Cernava, T., Champomier Vergès, M.-C., Charles, T., Chen, X., Cocolin, L., Eversole, K., Herrero Corral, G., Kazou, M., Kinkel, L., Lange, L., Lima, N., Loy, A., Macklin, J. A., Maguin, E., Mauchline, T., McClure, R., Mitter, B., … Schloter, M. (2020). Microbiome definition re-visited: Old concepts and new challenges. Microbiome, 8(1), 103. https://doi.org/10.1186/s40168-020-00875-0
7. Bhimani, P., Mahavar, P., Rajguru, B., Bhatt, V. D., Nathani, N. M., & Shri, M. (2024). Unveiling the green dialogue: advancements in omics technologies for deciphering plant–microbe interactions in soil. Discover Plants, 1(1), 4. https://doi.org/10.1007/s44372-024-00004-3
8. Brown, R. W., Reay, M. K., Centler, F., Chadwick, D. R., Bull, I. D., McDonald, J. E., ... & Jones, D. L. (2024). Soil metabolomics-current challenges and future perspectives. Soil Biology and Biochemistry, 193, 109382. https://doi.org/10.1016/j.soilbio.2024.109382
9. Castellano-Hinojosa, A., & Strauss, S. L. (2021). Insights into the taxonomic and functional characterization of agricultural crop core rhizobiomes and their potential microbial drivers. Scientific Reports, 11(1), 10068. https://doi.org/10.1038/s41598-021-89569-7
10. Chakrovarty, A., Singh, A. K., & Pandey, A. K. (2026). Beneficial Microbes in Plant Salinity Stress Responses: Integrating Correlative Evidence With Mechanistic Frameworks. Physiologia Plantarum, 178(3), e70930. https://doi.org/10.1111/ppl.70930
11. Chen, Y., & Zhou, X. (2024). Symbiotic nitrogen fixation: The role of rhizobia in enhancing legume growth and soil fertility. Molecular Microbiology Research, 14. http://dx.doi.org/10.5376/mmr.2024.14.0012
12. Chesneau, G., Herpell, J., Garrido-Oter, R., & Hacquard, S. (2025). From synthetic communities to synthetic ecosystems: exploring causalities in plant–microbe–environment interactions. New Phytologist, 245(2), 496-502. https://doi.org/10.1111/nph.20250

13. Chetty, A., & Blekhman, R. (2024). Multi-omic approaches for host-microbiome data integration. Gut microbes, 16(1), 2297860. https://doi.org/10.1080/19490976.2023.2297860
14. Dao, T. M. L., & Ho, V. T. (2026). Why Bacterial Biocontrol Often Fails in the Field: Insights from Tomato Bacterial Disease Management in Tropical Systems with Emphasis on Vietnam. Applied Biosciences, 5(3), 52. https://doi.org/10.3390/applbiosci5030052
15. De Souza, R. S. C., Armanhi, J. S. L., & Arruda, P. (2020). From microbiome to traits: designing synthetic microbial communities for improved crop resiliency. Frontiers in plant science, 11, 1179. https://doi.org/10.3389/fpls.2020.01179
16. Deng, S., Caddell, D. F., Xu, G., Dahlen, L., Washington, L., Yang, J., & Coleman-Derr, D. (2021). Genome wide association study reveals plant loci controlling heritability of the rhizosphere microbiome. The ISME journal, 15(11), 3181-3194. https://doi.org/10.1038/s41396-021-00993-z
17. Dhiman, I., Poria, V., Kumar, S., Yadav, R., Shaik, T., Bedwal, S., & Wati, L. (2026). Plant growth promoting rhizobacteria (PGPR) mediated amelioration of plant tolerance to abiotic stresses: Drought, salinity, and heavy metals. Archives of Microbiology, 208(2), 100. https://doi.org/10.1007/s00203-025-04631-6
18. Diwan, D., Rashid, M. M., & Vaishnav, A. (2022). Current understanding of plant-microbe interaction through the lenses of multi-omics approaches and their benefits in sustainable agriculture. Microbiological research, 265, 127180. https://doi.org/10.1016/j.micres.2022.127180
19. Dong, Q., Su, H., Sun, Y., Zhao, Y., Zhou, D., Wang, X., ... & Yu, H. (2024). Metagenomic insights into nitrogen cycling functional gene responses to nitrogen fixation and transfer in maize–peanut intercropping. Plant, cell & environment, 47(12), 4557-4571. https://doi.org/10.1111/pce.15034
20. Du, T., Hu, Q., Mao, W., Yang, Z., Chen, H., Sun, L., & Zhai, M. (2023). Metagenomics insights into the functional profiles of soil carbon, nitrogen, and phosphorus cycles in a walnut orchard under various regimes of long-term fertilisation. European Journal of Agronomy, 148, 126887. https://doi.org/10.1016/j.eja.2023.126887
21. Ece, G., Aktaş, A., Koyuncu Özyurt, Ö., Demirbakan, H., Alışkan, H. E., Sağlık, İ., ... & Kula Atik, T. (2026). Basic Microbiome Analysis: Analytical Steps from Sampling to Sequencing. Microorganisms, 14(2), 387. https://doi.org/10.3390/microorganisms14020387
22. Ejaz, M. R., Badr, K., Hassan, Z. U., Al-Thani, R., & Jaoua, S. (2024). Metagenomic approaches and opportunities in arid soil research. Science of The Total Environment, 953, 176173. https://doi.org/10.1016/j.scitotenv.2024.176173
23. Escudero-Martinez, C., & Bulgarelli, D. (2023). Engineering the crop microbiota through host genetics. Annual Review of Phytopathology, 61(1), 257-277. https://doi.org/10.1146/annurev-phyto-021621-121447
24. Etesami, H. (2026). Microbial necromass as the central architect of soil carbon: Reconciling plant inputs, microbial processing, and mineral stabilization in a critical synthesis. Sustainable Chemistry for Climate Action, 100221. https://doi.org/10.1016/j.scca.2026.100221
25. Etesami, H., Noori, F., Ebadi, A., & Reiahi Samani, N. (2020). Alleviation of stress-induced ethylene-mediated negative impact on crop plants by bacterial ACC deaminase: perspectives and applications in stressed agriculture management. Plant microbiomes for sustainable agriculture, 287-315. https://doi.org/10.1007/978-3-030-38453-1_10
26. Fadiji, A. E., Xiong, C., Egidi, E., & Singh, B. K. (2024). Formulation challenges associated with microbial biofertilizers in sustainable agriculture and paths forward. Journal of Sustainable Agriculture and Environment, 3(3), e70006. https://doi.org/10.1002/sae2.70006
27. Falk, N. W., Droppo, I. G., Drouillard, K. G., & Weisener, C. G. (2025). Combined DNA/RNA Amplicon Sequencing and Metatranscriptomics Reveals Microbial-Driven Nutrient Transformations and Core Taxa in Agriculturally Impacted Sediments. Environmental Microbiology Reports, 17(5), e70205. https://doi.org/10.1111/1758-2229.70205
28. Feng, Y., Tang, Y., Abdoulaye, A. H., Zhang, Y., Wen, W., Wang, H., ... & Chen, Y. (2026). Progress in plant rhizosphere microbiome research for improved growth, nutrient uptake, and disease resistance. Plant Stress, 101323. https://doi.org/10.1016/j.stress.2026.101323
29. Fernandes, M., & Husi, H. (2019). Integrative Systems Biology Resources and Approaches in. Systems Biology, 11. https://doi.org/10.5772/intechopen.84834
30. Fernández-Triana, I., Rubilar, O., Parada, J., Fincheira, P., Benavides-Mendoza, A., Durán, P., ... & Tortella, G. R. (2024). Metal nanoparticles and pesticides under global climate change: assessing the combined effects of multiple abiotic stressors on soil microbial ecosystems. Science of The Total Environment, 942, 173494. https://doi.org/10.1016/j.scitotenv.2024.173494
31. Feussner, I., & Polle, A. (2015). What the transcriptome does not tell—proteomics and metabolomics are closer to the plants' patho-phenotype. Current opinion in plant biology, 26, 26-31. https://doi.org/10.1016/j.pbi.2015.05.023
32. Hemme, C. L., Atoyan, J., Cai, A., & Liu, C. (2026). Challenges and Opportunities in Multi-Omics Data Acquisition and Analysis: Toward Integrative Solutions. Biomolecules, 16(2), 271. https://doi.org/10.3390/biom16020271
33. Hernández-García, J. A., Bernal, J. S., Antony-Babu, S., Villa-Tanaca, L., Hernández-Rodríguez, C., & De-la-Vega-Camarillo, E. (2025). Teosinte-derived SynCom and precision biofertilization modulate the maize

microbiome, enhancing growth, yield, and soil functionality in a Mexican field. Frontiers in Microbiology, 16, 1534327. https://doi.org/10.3389/fmicb.2025.1534327
34. Hicks, L. C., Frey, B., Kjøller, R., Lukac, M., Moora, M., Weedon, J. T., & Rousk, J. (2022). Toward a function-first framework to make soil microbial ecology predictive. Ecology, 103(2), e03594. https://doi.org/10.5194/egusphere-egu21-14139, https://doi.org/10.1128/msystems.01116-20
35. Irfan, M. F., Shafique, S., Shafique, S., Tabassum, B., & Yaseen, A. R. (2026). Molecular pathways in plant growth-promoting rhizobacteria–plant interactions: a comprehensive review. Archives of Microbiology, 208(4), 205. https://doi.org/10.1007/s00203-026-04749-1
36. Irineu, L. E. S. D. S., Soares, C. D. P., Soares, T. S., Almeida, F. A. D., Almeida-Silva, F., Gazara, R. K., ... & Olivares, F. L. (2022). Multiomic approaches reveal hormonal modulation and nitrogen uptake and assimilation in the initial growth of maize inoculated with Herbaspirillum seropedicae. Plants, 12(1), 48. https://doi.org/10.3390/plants12010048
37. Jansson, J. K., & Hofmockel, K. S. (2018). The soil microbiome—from metagenomics to metaphenomics. Current opinion in microbiology, 43, 162-168. https://doi.org/10.1016/j.mib.2018.01.013
38. Jia, J., de Goede, R., Li, Y., Zhang, J., Wang, G., Zhang, J., & Creamer, R. (2025). Unlocking soil health: Are microbial functional genes effective indicators?. Soil Biology and Biochemistry, 204, 109768. https://doi.org/10.1016/j.soilbio.2025.109768
39. Joos, L., Ommeslag, S., Baeyen, S., Asselberg, W., Van Loo, K., Clement, L., ... & De Tender, C. (2025). Year-long, multiple-timepoint field studies show the importance of spatiotemporal dynamics and microbial functions in agricultural soil microbiomes. Msystems, 10(7), e00112-25. https://doi.org/10.1128/msystems.00112-25
40. Keck, F., Couton, M., & Altermatt, F. (2023). Navigating the seven challenges of taxonomic reference databases in metabarcoding analyses. Molecular Ecology Resources, 23(4), 742-755. https://doi.org/10.1111/1755-0998.13746
41. Köhl, J. (2025). Use of beneficial microorganisms in crop production: do current regulatory frameworks in the EU fit for purpose? J. Köhl. BioControl, 70(4), 433-450. https://doi.org/10.1007/s10526-025-10326-0
42. Kumar Sarker, A., Kuar, K. D., Kuriakose, E., Morton, C. O., Stack, C. M., & Moffitt, M. C. (2026). Beyond the single isolate: leveraging plant-associated microbial communities for crop resilience. Microorganisms, 14(2), 456. https://doi.org/10.3390/microorganisms14020456
43. Kumar, S. M., Ragupathy, T. V., Dananjeyan, B., Thiyagarajan, C., Loganathan, A., & Natarajan, S. (2026). Microbiome-assisted plant breeding: integrating host-microbiome interactions into crop improvement. Archives of Microbiology, 208(5), 242. https://doi.org/10.1007/s00203-026-04795-9
44. Latz, E., Eisenhauer, N., Rall, B. C., Scheu, S., & Jousset, A. (2016). Unravelling linkages between plant community composition and the pathogen-suppressive potential of soils. Scientific Reports, 6(1), 23584. https://doi.org/10.1038/srep23584
45. Laudadio, I., Fulci, V., Palone, F., Stronati, L., Cucchiara, S., & Carissimi, C. (2018). Quantitative assessment of shotgun metagenomics and 16S rDNA amplicon sequencing in the study of human gut microbiome. OMICS: A Journal of Integrative Biology, 22(4), 248-254. https://doi.org/10.1089/omi.2018.0013
46. Leite, M. F., van den Broek, S. W., & Kuramae, E. E. (2022). Current challenges and pitfalls in soil metagenomics. Microorganisms, 10(10), 1900. https://doi.org/10.3390/microorganisms10101900
47. Li, S., Chiodi, C., Maucieri, C., Della Lucia, M. C., Zardinoni, G., Ravi, S., ... & Stevanato, P. (2026). Profiling soil–plant–microbial communities: DNA and multi-omics techniques. Genes, 17(3), 303. https://doi.org/10.3390/genes17030303
48. Li, W. X., Wang, C., Zheng, M. M., Cai, Z. J., Wang, B. R., & Shen, R. F. (2020). Fertilization strategies affect soil properties and abundance of N-cycling functional genes in an acidic agricultural soil. Applied Soil Ecology, 156, 103704. https://doi.org/10.1016/j.apsoil.2020.103704
49. Liang, X., Yu, S., Ju, Y., Wang, Y., & Yin, D. (2025). Multi-scale remote-sensing phenomics integrated with multi-omics: Advances in crop drought–heat stress tolerance mechanisms and perspectives for climate-smart agriculture. Plants, 14(18), 2829. https://doi.org/10.3390/plants14182829
50. Liu, C. W., & Murray, J. D. (2016). The role of flavonoids in nodulation host-range specificity: an update. Plants, 5(3), 33. https://doi.org/10.3390/plants5030033
51. Liu, Y., Beyer, A., & Aebersold, R. (2016). On the dependency of cellular protein levels on mRNA abundance. Cell, 165(3), 535-550. https://doi.org/10.1016/j.cell.2016.03.014
52. Lobo, C. B., Tomás, M. S. J., Viruel, E., Ferrero, M. A., & Lucca, M. E. (2019). Development of low-cost formulations of plant growth-promoting bacteria to be used as inoculants in beneficial agricultural technologies. Microbiological research, 219, 12-25. https://doi.org/10.1016/j.micres.2018.10.012
53. Louca, S., Polz, M. F., Mazel, F., Albright, M. B., Huber, J. A., O'Connor, M. I., ... & Parfrey, L. W. (2018). Function and functional redundancy in microbial systems. Nature ecology & evolution, 2(6), 936-943. https://doi.org/10.1038/s41559-018-0519-1
54. Madhulika, C. K., Dowarah, B., Bisen, P., Banerjee, S., & Dinkar, S. (2025). Soil microbiome dynamics and their role in sustainable agriculture. https://www.doi.org/10.33545/2618060X.2025.v8.i4f.2811
55. Mahapatra, B., Ghosh, D., & Mukhopadhyay, R. (2024). Biocontrol potential of Trichoderma and Pseudomonas: A review. Int. J. Adv. Biochem. Res, 8, 129-132.

https://doi.org/10.33545/26174693.2024.v8.i4Sb.933
56. Manor, O., & Borenstein, E. (2017). Revised computational metagenomic processing uncovers hidden and biologically meaningful functional variation in the human microbiome. Microbiome, 5(1), 19. https://doi.org/10.1186/s40168-017-0231-4
57. Martins, G. L., Monteiro, G. G. T. N., Lange, M., de Freitas, A. S., do Nascimento Silva Barbosa, L., van Leeuwen, J., ... & Tsai, S. M. (2026). Land-use intensification reshapes microbial phosphorus cycling, organic matter composition, and phosphorus fractions in Amazonian soils. ISME communications, 6(1), ycag027. https://doi.org/10.1093/ismeco/ycag027
58. Mawarda, P. C., Le Roux, X., Van Elsas, J. D., & Salles, J. F. (2020). Deliberate introduction of invisible invaders: a critical appraisal of the impact of microbial inoculants on soil microbial communities. Soil Biology and Biochemistry, 148, 107874. https://doi.org/10.1016/j.soilbio.2020.107874
59. Miransari, M. (2013). Arbuscular mycorrhizal fungi and uptake of nutrients. In Symbiotic endophytes (pp. 253-270). Berlin, Heidelberg: Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-39317-4_13
60. Mirete, S., Sánchez-Costa, M., Díaz-Rullo, J., González de Figueras, C., Martínez-Rodríguez, P., & González-Pastor, J. E. (2025). Metagenome-assembled genomes (MAGs): advances, challenges, and ecological insights. Microorganisms, 13(5), 985. https://doi.org/10.3390/microorganisms13050985
61. Morales, S. E., & Holben, W. E. (2011). Linking bacterial identities and ecosystem processes: can 'omic'analyses be more than the sum of their parts?. FEMS microbiology ecology, 75(1), 2-16. https://doi.org/10.1111/j.1574-6941.2010.00938.x
62. Moshood, A. Y., Abdulraheem, M. I., Li, L., Zhang, Y., Raghavan, V., & Hu, J. (2025). Deciphering nutrient stress in plants: integrative insight from metabolomics and proteomics. Functional & Integrative Genomics, 25(1), 38. https://doi.org/10.1007/s10142-025-01551-y
63. Mukherjee, A., & Reddy, M. S. (2020). Metatranscriptomics: an approach for retrieving novel eukaryotic genes from polluted and related environments. 3 Biotech, 10(2), 71. https://doi.org/10.1007/s13205-020-2057-1
64. Negre Rodríguez, M., Pioppi, A., & Kovács, Á. T. (2025). The role of plant host genetics in shaping the composition and functionality of rhizosphere microbiomes. Msystems, 10(8), e00041-24. https://doi.org/10.1128/msystems.00041-24
65. O'Neal, L., Vo, L., & Alexandre, G. (2020). Specific root exudate compounds sensed by dedicated chemoreceptors shape Azospirillum brasilense chemotaxis in the rhizosphere. Applied and Environmental Microbiology, 86(15), e01026-20. https://doi.org/10.1128/AEM.01026-20
66. Overy, D. P., Bell, M. A., Habtewold, J., Helgason, B. L., & Gregorich, E. G. (2021). "Omics" technologies for the study of soil carbon stabilization: a review. Frontiers in Environmental Science, 9, 617952. https://doi.org/10.3389/fenvs.2021.617952
67. Pacheco-Moreno, A., Bollmann-Giolai, A., Chandra, G., Brett, P., Davies, J., Thornton, O., ... & Malone, J. G. (2024). The genotype of barley cultivars influences multiple aspects of their associated microbiota via differential root exudate secretion. PLoS Biology, 22(3), e3002232. https://doi.org/10.1371/journal.pbio.3002232
68. Pan, H., Wattiez, R., & Gillan, D. (2024). Soil Metaproteomics for Microbial Community Profiling: Methodologies and Challenges: H. Pan et al. Current Microbiology, 81(8), 257. https://doi.org/10.1007/s00284-024-03781-y
69. Pandey, K., & Saharan, B. S. (2025). Soil microbiomes: a promising strategy for boosting crop yield and advancing sustainable agriculture. Discover Agriculture, 3(1), 54. https://doi.org/10.1007/s44279-025-00208-5
70. Pandit, B., Bohara, C. B., Shrestha, S., & Acharya, R. (2026). Rhizosphere microbial communities: Drivers of nutrient cycling, plant health, and soil fertility. Archives of Agriculture and Environmental Science, 11(2), 248-255. https://doi.org/10.26832/24566632.2026.1102015
71. Pang, F., Li, Q., Solanki, M. K., Wang, Z., Xing, Y. X., & Dong, D. F. (2024). Soil phosphorus transformation and plant uptake driven by phosphate-solubilizing microorganisms. Frontiers in Microbiology, 15, 1383813. https://doi.org/10.3389/fmicb.2024.1383813
72. Parveen, S., Shafi, Z., Shahid, M., Iqbal, M. Z., Naznine, F., & Ansari, M. I. (2026). Omics-Driven Insights Into Soil Microbial Diversity and Phytopathogen Interactions for Sustainable Agriculture and Food Security. Journal of Basic Microbiology, 66(2), e70155. https://doi.org/10.1002/jobm.70155
73. Pedersen, H. K., Forslund, S. K., Gudmundsdottir, V., Petersen, A. Ø., Hildebrand, F., Hyötyläinen, T., ... & Nielsen, H. B. (2018). A computational framework to integrate high-throughput '-omics' datasets for the identification of potential mechanistic links. Nature protocols, 13(12), 2781-2800. https://doi.org/10.1038/s41596-018-0064-z
74. Pérez-Cobas, A. E., Gomez-Valero, L., & Buchrieser, C. (2020). Metagenomic approaches in microbial ecology: an update on whole-genome and marker gene sequencing analyses. Microbial genomics, 6(8), e000409. https://doi.org/10.1099/mgen.0.000409
75. Preheim, S. P., Morris, S., Zhang, Y., Holder, C., Arora-Williams, K., Gensbigler, P., ... & Gnanadesikan, A. (2025). Genes involved in carbon, nitrogen, and sulfur cycling in an important estuarine ecosystem show coherent shifts in response to changes in environmental conditions. Limnology and Oceanography, 70(1), 25-39. https://doi.org/10.1002/lno.12731

76. Ramirez-Villacis, D. X., Leon-Reyes, A., Pieterse, C. M., & Raaijmakers, J. M. (2025). Born to rewild: Reconnecting beneficial plant-microbiome alliances for resilient future crops. Cell Host & Microbe, 33(8), 1241-1255. https://doi.org/10.1016/j.chom.2025.06.017
77. Rempfert, K. R., Bell, S. L., Kasanke, C. P., Zhao, Q., Zhao, X., Lipton, A. S., & Hofmockel, K. S. (2024). Biomolecular budget of persistent, microbial-derived soil organic carbon: The importance of underexplored pools. Science of the Total Environment, 932, 172916. https://doi.org/10.1016/j.scitotenv.2024.172916
78. Rincon-Florez, V. A., Carvalhais, L. C., & Schenk, P. M. (2013). Culture-independent molecular tools for soil and rhizosphere microbiology. Diversity, 5(3), 581-612. https://doi.org/10.3390/d5030581
79. Rizaludin, M. S., Stopnisek, N., Raaijmakers, J. M., & Garbeva, P. (2021). The chemistry of stress: understanding the 'cry for help'of plant roots. Metabolites, 11(6), 357. https://doi.org/10.3390/metabo11060357
80. Robert, C. A. M., Himmighofen, P., McLaughlin, S., Cofer, T. M., Khan, S. A., Siffert, A., & Sasse, J. (2025). Environmental and biological drivers of root exudation. Annual Review of Plant Biology, 76. https://doi.org/10.1146/annurev-arplant-083123-082752
81. Roller, M., Lucić, V., Nagy, I., Perica, T., & Vlahoviček, K. (2013). Environmental shaping of codon usage and functional adaptation across microbial communities. Nucleic acids research, 41(19), 8842-8852. https://doi.org/10.1093/nar/gkt673
82. Roy, S., Soumen, S., Arp, J. T., Kaur, J., Bhowmick, R., Pettit, T., ... & Sanyal, D. (2026). From soil to sequences: mechanisms and tools unravelling plant-rhizomicrobiome interactions. World Journal of Microbiology and Biotechnology, 42(3), 127. https://doi.org/10.1007/s11274-026-04865-6
83. Sabale, S. N., Suryawanshi, P. P., & Krishnaraj, P. U. (2019). Soil metagenomics: concepts and applications. Metagenomics-basics, methods and applications, 10. https://www.intechopen.com/chapters/70015
84. Sahoo, A., Yadav, G., Mehta, T., Meena, M., & Swapnil, P. (2025). Omics-driven insights into plant growth-promoting microorganisms for sustainable agriculture. Discover Sustainability, 6(1), 659. https://doi.org/10.1007/s43621-025-01582-2
85. Sahoo, H., Kisku, K., & Naik, U. C. (2021). Application of Omics Tools for Microbial Community Structure and Function Analysis. In Wastewater Treatment (pp. 433-456). Elsevier. https://doi.org/10.1016/B978-0-12-821881-5.00021-0
86. Sanches, P. H. G., de Melo, N. C., Porcari, A. M., & de Carvalho, L. M. (2024). Integrating molecular perspectives: strategies for comprehensive multi-omics integrative data analysis and machine learning applications in transcriptomics, proteomics, and metabolomics. Biology, 13(11), 848. https://doi.org/10.3390/biology13110848
87. Sardar, P., Almeida, A., & Pedicord, V. A. (2024). Integrating functional metagenomics to decipher microbiome–immune interactions. Immunology and Cell Biology, 102(8), 680-691. https://doi.org/10.1111/imcb.12798
88. Schlatter, D., Kinkel, L., Thomashow, L., Weller, D., & Paulitz, T. (2017). Disease suppressive soils: new insights from the soil microbiome. Phytopathology, 107(11), 1284-1297. https://doi.org/10.1094/PHYTO-03-17-0111-RVW
89. Shaffer, J. P., Nothias, L. F., Thompson, L. R., Sanders, J. G., Salido, A., Couvillion, S. P., ... & Dorrestein, P. C. (2022). Standardized multi-omics of Earth's microbiomes reveals microbial and metabolite links. Nature Microbiology, 7(12), 2128–2150. https://doi.org/10.1038/s41564-022-01266-x
90. Shah, A. S., Zaman, M. A. U., Burgess, T. I., & Bayliss, K. L. (2025). Different soil sampling designs influence the diversity and drivers of the avocado rhizosphere bacterial and fungal communities. Applied Soil Ecology, 214, 106391. https://doi.org/10.1016/j.apsoil.2025.106391
91. Shahmohamadloo, R. S., Febria, C. M., Fraser, E. D., & Sibley, P. K. (2021). The sustainable agriculture imperative: A perspective on the need for an agrosystem approach to meet the United Nations Sustainable Development Goals by 2030. Integrated Environmental Assessment and Management, 18(5), 1199-1205. https://doi.org/10.1002/ieam.4558
92. Shittu, O. E., Enagbonma, B. J., & Babalola, O. O. (2026). Exploring Multifunctional Microbial Genes From the Rhizosphere of Allium ampeloprasum Under Different Fertilization Systems. Environmental DNA, 8(2), e70275. https://doi.org/10.1002/edn3.70275
93. Shrestha, H. K., Appidi, M. R., Villalobos Solis, M. I., Wang, J., Carper, D. L., Burdick, L., ... & Abraham, P. E. (2021). Metaproteomics reveals insights into microbial structure, interactions, and dynamic regulation in defined communities as they respond to environmental disturbance. BMC microbiology, 21(1), 308. https://doi.org/10.1186/s12866-021-02370-4
94. Sibanyoni, N. R., Mmotla, K., Mashabela, M. D., Piater, L. A., Kerchev, P., & Mhlongo, M. I. (2025). Chemical dialogues in the rhizosphere: Metabolomics perspectives on plant defence and microbial interactions. Plant and soil, 1-27. https://doi.org/10.1007/s11104-025-08010-4
95. Sible, C. N., Seebauer, J. R., & Below, F. E. (2025). Biostimulant or biological? The complexity of defining, categorizing, and regulating microbial inoculants. Agricultural & Environmental Letters, 10(2), e70027. https://doi.org/10.1002/ael2.70027
96. Siles, J. A., Starke, R., Martinovic, T., Fernandes, M. L. P., Orgiazzi, A., & Bastida, F. (2022). Distribution of phosphorus cycling genes across land uses and microbial taxonomic groups based on metagenome and genome mining. Soil Biology and Biochemistry, 174, 108826. https://doi.org/10.1016/j.soilbio.2022.108826

97. Singh, M., Jha, S., Pathak, D., & Maisnam, G. (2025). Advancing biofertilizers: the evolution from single-strain formulations to synthetic microbial communities (SynCom) for sustainable agriculture. Discover Plants, 2(1), 226. https://doi.org/10.1007/s44372-025-00318-w
98. Singh, R. P., Ma, Y., & Shadan, A. (2022). Perspective of ACC-deaminase producing bacteria in stress agriculture. Journal of Biotechnology, 352, 36-46. https://doi.org/10.1016/j.jbiotec.2022.05.002
99. Sivasakthi, S., Usharani, G., & Saranraj, P. (2014). Biocontrol potentiality of plant growth promoting bacteria (PGPR)-Pseudomonas fluorescens and Bacillus subtilis: A review. Afr. J. Agric. Res, 9(16), 1265-1277. https://doi.org/10.5897/AJAR2013.7914
100. Slaughter, L. (2021). Rhizosphere. In Principles and applications of soil microbiology (pp. 269-301). Elsevier. https://doi.org/10.1016/B978-0-12-820202-9.00011-3
101. Smercina, D. N., Evans, S. E., Friesen, M. L., & Tiemann, L. K. (2019). To fix or not to fix: controls on free-living nitrogen fixation in the rhizosphere. Applied and Environmental Microbiology, 85(6), e02546-18. https://doi.org/10.1128/AEM.02546-18
102. Song, C., Zhu, F., Carrión, V. J., & Cordovez, V. (2020). Beyond plant microbiome composition: exploiting microbial functions and plant traits via integrated approaches. Frontiers in Bioengineering and Biotechnology, 8, 896. https://doi.org/10.3389/fbioe.2020.00896
103. Song, P., Deng, Y., Yu, Y., Zhang, L., & Liu, Y. (2026). Plant Growth-Promoting Microorganisms Mediate Plant Metabolic Reprogramming to Manage the Rhizospheric Microbiome. Microorganisms, 14(3), 578. https://doi.org/10.3390/microorganisms14030578
104. Spooren, J., van Bentum, S., Thomashow, L. S., Pieterse, C. M., Weller, D. M., & Berendsen, R. L. (2024). Plant-driven assembly of disease-suppressive soil microbiomes. Annual Review of Phytopathology, 62(1), 1-30. https://doi.org/10.1146/annurev-phyto-021622-100127
105. Srivastava, N., & Sarethy, I. P. (2021). Rhizosphere Fingerprints: Novel Biomolecules Via Meta-Omics Technology. In Omics Science for Rhizosphere Biology (pp. 171-188). Singapore: Springer Singapore. https://doi.org/10.1007/978-981-16-0889-6_10
106. Starke, R., Jehmlich, N., & Bastida, F. (2019). Using proteins to study how microbes contribute to soil ecosystem services: the current state and future perspectives of soil metaproteomics. Journal of Proteomics, 198, 50-58. https://doi.org/10.1016/j.jprot.2018.11.011
107. Sudarshan, S., Niveditha, M. P., Alekhya Gunturi, S., Chethan Babu, R. T., & KB, C. K. (2024). Effects of intensive agricultural management practices on soil biodiversity and implications for ecosystem functioning: A review. Int. J. Res. Agron, 7, 166-169. https://doi.org/10.33545/2618060X.2024.v7.i9Sc.1446
108. Sun, R., Wang, F., Hu, C., & Liu, B. (2021). Metagenomics reveals taxon-specific responses of the nitrogen-cycling microbial community to long-term nitrogen fertilization. Soil Biology and Biochemistry, 156, 108214. https://doi.org/10.1016/j.soilbio.2021.108214
109. Sun, X., Tian, X., Jia, M., Hu, X., Zhang, C., & Zhao, L. (2026). Phosphate-solubilizing bacteria: a review of diversity, mechanisms, and applications in sustainable agriculture. Frontiers in Microbiology, 17, 1778470. https://doi.org/10.3389/fmicb.2026.1778470
110. Suresh, A., Ashraf, A. M., Sree, V. S., Dhas, A. K. S., & Chacko, J. P. (2025). Plant-microbe interactions and rhizosphere dynamics for sustainable agriculture: a review. AG, 1-9. https://arccjournals.com/journal/agricultural-reviews/R-2829
111. Suresh, G., Sharma, P., Dadrwal, B. K., Jat, R. K., Singh, V. P., Kumar, M., ... & Teja, M. S. V. R. (2025). Biochemical Interactions in the Rhizosphere: Roles of Root Exudates, Flavonoids and Phytoalexins in Plant–Microbe Communication. Plant Cell Biotechnology and Molecular Biology, 26(9-10), 270-279. https://doi.org/10.56557/pcbmb/2025/v26i9-109828
112. Syeda, A. (2025). Harnessing multi-omics and genome-editing technologies for climate-resilient agriculture: bridging AI-driven insights with sustainable crop improvement. Plant Molecular Biology, 115(6), 1-24. https://doi.org/10.1007/s11103-025-01650-1
113. Tarazona, S., Balzano-Nogueira, L., Gómez-Cabrero, D., Schmidt, A., Imhof, A., Hankemeier, T., ... & Conesa, A. (2020). Harmonization of quality metrics and power calculation in multi-omic studies. Nature communications, 11(1), 3092. https://doi.org/10.1038/s41467-020-16937-8
114. Tracanna, V., Ossowicki, A., Petrus, M. L., Overduin, S., Terlouw, B. R., Lund, G., ... & Medema, M. H. (2021). Dissecting disease-suppressive rhizosphere microbiomes by functional amplicon sequencing and 10× metagenomics. MSystems, 6(3), 10-1128.
115. Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T., & Singh, B. K. (2020). Plant–microbiome interactions: From community assembly to plant health. Nature Reviews Microbiology, 18(11), 607–621. https://doi.org/10.1038/s41579-020-0412-1
116. Tyagi, S., & Katara, P. (2024). Metatranscriptomics: a tool for clinical metagenomics. Omics: a journal of integrative biology, 28(8), 394-407. https://doi.org/10.1089/omi.2024.0130
117. Upadhyay, S. K., Singh, D. P., & Singh, J. S. (2022). Plant-microbe interactions in the rhizosphere: Mechanisms and applications for sustainable agriculture. Microbiological Research, 262, 127114. https://doi.org/10.1016/j.micres.2022.127114

118. Vinay, C. M., Udayamanoharan, S. K., Prabhu Basrur, N., Paul, B., & Rai, P. S. (2021). Current analytical technologies and bioinformatic resources for plant metabolomics data. Plant Biotechnology Reports, 15(5), 561-572. https://doi.org/10.1007/s11816-021-00703-3
119. Wang, P., Li, J. L., Luo, X. Q., Ahmad, M., Duan, L., Yin, L. Z., ... & Li, W. J. (2022). Biogeographical distributions of nitrogen-cycling functional genes in a subtropical estuary. Functional Ecology, 36(1), 187-201. https://doi.org/10.1111/1365-2435.13949
120. Wani, A. K., Qadir, F., Elboughdiri, N., Rahayu, F., Pranowo, D., Martasari, C., ... & Singh, R. (2025). Metagenomics and plant-microbe symbioses: microbial community dynamics, functional roles in carbon sequestration, nitrogen transformation, sulfur and phosphorus mobilization for sustainable soil health. Biotechnology Advances, 82, 108580. https://doi.org/10.1016/j.biotechadv.2025.108580
121. Wankhade, A., Wilkinson, E., Britt, D. W., & Kaundal, A. (2025). A review of plant–microbe interactions in the rhizosphere and the role of root exudates in microbiome engineering. Applied Sciences, 15(13), 7127. https://doi.org/10.3390/app15137127
122. Withers, E., Hill, P. W., Chadwick, D. R., & Jones, D. L. (2020). Use of untargeted metabolomics for assessing soil quality and microbial function. Soil Biology and Biochemistry, 143, 107758. https://doi.org/10.1016/j.soilbio.2020.107758
123. Wolfgang, A., Zachow, C., Müller, H., Grand, A., Temme, N., Tilcher, R., & Berg, G. (2020). Understanding the impact of cultivar, seed origin, and substrate on bacterial diversity of the sugar beet rhizosphere and suppression of soil-borne pathogens. Frontiers in Plant Science, 11, 560869. https://doi.org/10.3389/fpls.2020.560869
124. Wu, H., Wan, S., Ruan, C., Wan, W., Han, M., Chen, G., ... & Wang, G. (2023). Soil microbial necromass: The state-of-the-art, knowledge gaps, and future perspectives. European Journal of Soil Biology, 115, 103472. https://doi.org/10.1016/j.ejsobi.2023.103472
125. Wu, X., Rensing, C., Han, D., Xiao, K. Q., Dai, Y., Tang, Z., ... & Zhang, F. (2022). Genome-resolved metagenomics reveals distinct phosphorus acquisition strategies between soil microbiomes. Msystems, 7(1), e01107-21. https://doi.org/10.1128/msystems.01107-21
126. Xu, Y., Shrestha, S., Sun, Q., & Wang, Y. (2026). Roles of microbial interactions in determining the establishment and function of synthetic consortium inoculants for soil applications. The ISME Journal, 20(1), wrag050. https://doi.org/10.1093/ismejo/wrag050
127. Yan, C., Zhang, F., Long, C., Yin, Y., & Wang, L. (2026). A Brief Review of Microbial Omics: Methods and Perspectives. Microbial 'Omics: Methods and Protocols, 1-20. https://doi.org/10.1007/978-1-0716-5264-0_1
128. Yang, Q., Aghdam, R., Tran, P. Q., Anantharaman, K., & Solís-Lemus, C. (2026). Activity-Informed Network Analysis Reveals Keystone Microbes Shaping Freshwater Ecosystem Function. Environmental Microbiology Reports, 18(2), e70245. https://doi.org/10.1111/1758-2229.70245
129. Yu, K., Pieterse, C. M., Bakker, P. A., & Berendsen, R. L. (2019). Beneficial microbes going underground of root immunity. Plant, cell & environment, 42(10), 2860-2870. https://doi.org/10.1111/pce.13632
130. Yu, X., Feng, B., He, P., & Shan, L. (2017). From chaos to harmony: responses and signaling upon microbial pattern recognition. Annual review of phytopathology, 55(1), 109-137. https://doi.org/10.1146/annurev-phyto-080516-035649
131. Yu, Y., Gui, Y., Li, Z., Jiang, C., Guo, J., & Niu, D. (2022). Induced systemic resistance for improving plant immunity by beneficial microbes. Plants, 11(3), 386. https://doi.org/10.3390/plants11030386
132. Zaramela, L. S., Moyne, O., Kumar, M., Zuniga, C., Tibocha-Bonilla, J. D., & Zengler, K. (2021). The sum is greater than the parts: exploiting microbial communities to achieve complex functions. Current Opinion in Biotechnology, 67, 149-157. https://doi.org/10.1016/j.copbio.2021.01.013
133. Zhalnina, K., Louie, K. B., Hao, Z., Mansoori, N., Da Rocha, U. N., Shi, S., ... & Brodie, E. L. (2018). Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. Nature microbiology, 3(4), 470-480. https://doi.org/10.1038/s41564-018-0129-3
134. Zhang, W., Li, F., & Nie, L. (2010). Integrating multiple 'omics' analysis for microbial biology: application and methodologies. Microbiology, 156(2), 287-301. https://doi.org/10.1099/mic.0.034793-0
135. Zhang, Y., Jing, M., Lyu, L., Nie, L., Xu, X., Sun, R., ... & Chu, H. (2026). Principles for rigorous design and application of synthetic microbial communities. Advanced Science, 13(10), e14750. https://doi.org/10.1002/advs.202514750
136. Zhou, R., Liu, Y., Dungait, J. A. J., Kumar, A., Wang, J., Tiemann, L. K., Zhang, F., Kuzyakov, Y., & Tian, J. (2023). Microbial necromass in cropland soils: A global meta-analysis of management effects. Global Change Biology, 29, 1998–2014. https://doi.org/10.1111/gcb.16613