PLANT SCIENCE TODAY
Vol 12(sp4): 01–13
https://doi.org/10.14719/pst.10229

eISSN 2348-1900

REVIEW ARTICLE

Role of microbiome associations in developing high yield and sustainable rice varieties

Prasanna P[1], Subrahmaniyan K[2], Arulmozhi R[3], Parthasarathi R[4], Rajarathinam P[2], Puspha R[3] & Dhandapani M[3]*

[1]Department of Genetics and Plant Breeding, Anbil Dharmaingam Agricultural College and Research Institute, Trichy 620 027, Tamil Nadu, India
[2]Department of Agronomy, Tamil Nadu Rice Research Institute, Aduthurai, Thanjavur 612 101, Tamil Nadu, India
[3]Department of Genetics and Plant Breeding, Tamil Nadu Rice Research Institute, Aduthurai, Thanjavur 612 101, Tamil Nadu, India
[4]Department of Soil Science, Anbil Dharmaingam Agricultural College and Research Institute, Trichy 620 027, Tamil Nadu, India

*Correspondence email - dhandapanim@tnau.ac.in

Received: 24 June 2025; Accepted: 25 July 2025; Available online: Version 1.0: 24 October 2025

Cite this article: Prasanna P, Subrahmaniyan K, Arulmozhi R, Parthasarathi R, Rajarathinam P, Puspha R, Dhandapani M. Role of microbiome associations in developing high yield and sustainable rice varieties. Plant Science Today. 2025;12(sp4):01–13. https:/doi.org/10.14719/pst.10229

Abstract

Rice, the staple food crop of half of the world population, is challenged by biotic and abiotic stresses which affect its productivity. Sustainable rice production will ensure safeguard food security. It involves genetic background, climate and soil factors. Development of low-input response varieties by genetically associating microbiomes involved in functional activities of rice growth and development offers scope for sustainability. This review focuses on genetics influence on microbiome connections and use of these microbiome associations to create low-input responsive rice varieties. Root exudates from traditional varieties with specific traits and unique microbiomes associations can prove useful in developing low-input rice varieties. Analysis of functional traits such as nutrient mobilization, resistance to pests and adaptation for abiotic stresses in various germplasm lines can help identify suitable parent plants for breeding. Study of the genetic mechanisms of microbiome association through QTL mapping and transcriptomic analysis identifying the genomic regions regulating the microbiome-related traits. Traditional breeding methods, marker-assisted techniques and rapid generation advancement strategies can be used to develop lines for evaluation. It involves screening methods, identification of selection parameters, inheritance pattern and optimization of field plot conditions need to be considered while developing the superior varieties. The evaluation pattern will be studied in various trials for studying the genotype x environment interactions and better lines will be identified for varietal release. The low-input response rice variety will be able to deploy specific microbes for functional activities.

Keywords:genotype-microbiome interaction; low input rice varieties; microbiome-assisted breeding; microbiome heritability; root exudates; sustainable agriculture

Introduction

Rice serves as the main food source for over half of the global population. It is enjoyed in various cooked forms including boiled rice, gruels, pancakes (*dosa*) and steamed buns made from fermented batter (*idly*). As per 2022-23 FAO data, India ranks second in terms of rice production at the world map and has 47.8 million hectares of land dedicated to rice cultivation and covers regions from Kashmir to Tamil Nadu (1). The crop grows across different climatic zones and ecosystems including lowland and upland areas. The crop is grown via methods like transplanting and direct seeding. Generally, rice growth requires about 730 m^3 of water for getting a yield of about one metric tonne (2). Indian rice types are categorized under the *indica* subspecies. They show characteristics such as good height, tendency to lodge, sensitivity to light, grain shattering and low yield. Low productivity has been noted in *indica* varieties in both pre- and post-independence eras. A bulk of rice grains is imported from Myanmar to meet out the increasing demand.

Various strategies and approaches were followed to get enhanced rice yield. During green revolution, semi-dwarf rice varieties that are insensitive to light and have shorter growth period were developed and introduced to get higher yield. Use of fertilizers was also increased in high-yielding varieties that get increased rice production. More fertilizers and supplements for used to get high rice yield. The practice of rice farming became more intensive due to the extensive use of chemical fertilizers. Because of finding semi-dwarfing gene sd1, a mutant of the GA 20 oxidase gene (*Os20ox2*), which leads to fertilizer responsive and lodging resistances. Rice breeders intentionally selected fertilizer-responsive lines in their breeding programs, with most rice varieties responding positive to yield. Along with loss of nutrient acquisition traits, which led to high fertilizer usage. The indiscriminate usage of fertilizer in rice farming led to soil and water contamination as well as increased susceptibility of major rice pests such as the rice stem borer, leaf folder, brown plant hopper and increased incidence of diseases, blast and grain discoloration. All these resulted in severe yield losses and initiated the need to replace chemical pesticides due to increasing environmental concerns such as deterioration in soil health and heavy metal contamination (3) (Fig. 1). Rice is usually grown in flooded conditions, which facilitates the movement and accumulation of heavy metal/metalloids (from agricultural and industrial waste and other chemicals) in rice plants (4). The need for developing the other alternative strategies which are eco-friendly and contribute in maintaining high yield for longer duration was realized.

The role of plant-associated microbiomes is important for sustainable cultivation, especially within rhizosphere facilitate nutrient uptake, promote plant growth and provides resistance to biotic and abiotic stressors. The genetic basis of plant-microbe interactions can lead to the development of rice varieties that are not only tolerant to environmental stresses but also capable of thriving in contaminated soils, offering a dual benefit of improving crop yield and ensuring food safety in vulnerable populations. Analysing microbiomes followed by their colonization and strong genetic compatibility results in enhanced fitness through microbial association. This interaction positively impacts crop productivity by boosting the presence of nutrient transport genes. A high rate of association among microbial taxa, support the soil microbiome thus leading to increased yields (5). This strategy not only helps in increasing production and nutrient accumulation but also proves useful in curtailing abiotic stresses and works antagonistic to plant pathogens. The interaction between the microbiome in rice roots triggers the production of root exudates that facilitate the release of nutrients. Besides this low molecular weight organic acids and bio-chelating agents (phytosiderophores) also aid in nutrient accumulation. This interaction is more interconnected and complex in wild types of rice. More stable and diverse microbial communities exist in changing environments (6). Those m-gene responsive for interaction will help in future breeding programmes and enhancing the biocontrol potential (7–9).

The tall *indica* land races possess the ability to mobilize nutrients through their natural association with microbes at various levels for nitrogen, phosphorus, potassium, zinc and iron. The tall *indica* rice genotypes exhibit a stronger association with microbiomes compared to modern high-yielding semi-dwarf varieties (10,11).

This review examines the influence of rice genetic factors on the diversity of microbiomes and their role in promoting sustainability by providing a broad perspective, including genetic elements of characteristics and their heritability, as well as how domestication affects microbial interactions. Additionally, it highlights challenges in breeding and practical applications such as SynComs and nutrient availability. It also addresses recent advancements in rice research through “omics” methodologies and their associated challenges. The article stands out for its broad, practical and forward-thinking approach to microbiome-assisted rice improvement.

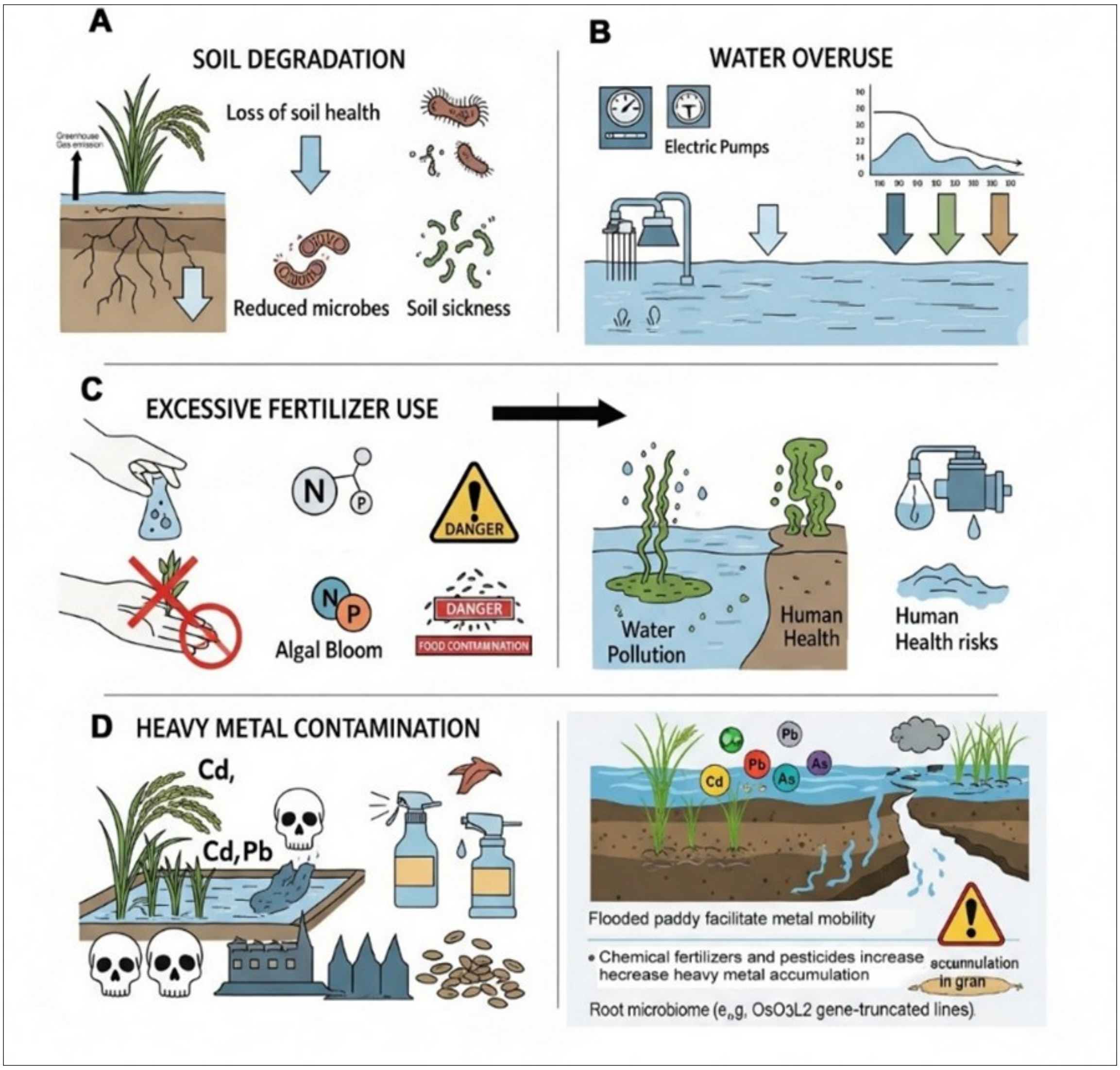

Fig. 1. Major issues related to present day rice cultivation.

Understanding the microbiome: a key to sustainable rice breeding

The microbiome is the community that contains bacteria, fungi, archaea and viruses. If we exclude viruses, it is termed microbiota (12). Another definition of microbiome given by Lederberg describes microbiomes within an ecological context as "a community of commensal, symbiotic and pathogenic microorganisms within a body space or other environment." The specific plant microbiome refers to the microbial communities that are linked to the plant and can exist, flourish and interact with various plant tissues, including roots, shoots, leaves, flowers and seeds (13). It is considered a priority to increase the sustainability of food production in the context of climate change in recent years (14). The plant microbiome can be differentiated into three parts: the phyllosphere, endosphere and rhizosphere (Fig. 2). This differentiation is based on the site where microorganisms are present and where interactions take place. If the microorganisms are present above ground, i.e. on plant surfaces like leaves, stems, flowers and fruit, this is referred to as the phyllosphere microbiome. Leaves are dominant part in context to phyllosphere (15,16). The phyllosphere contains bacteria, fungi, archaea, protists and viruses.

In rice, this community consist of mostly bacteria, fungi (6). Algae in the phyllosphere are considered to generate photosynthates for the use of heterotrophic microbes in the phyllosphere. In addition, they are involved in nitrogen mobilization, which is one of the major regulators of nutrient cycling. The part where the microbes are present in different plant tissues is known as the endosphere. The predominant function (up to 72 %) of the rice endophytic microbiome is to synthesize various biosynthetic products like amino acids, nucleosides and nucleotides, fatty acids, lipids, etc., followed by the production of precursor metabolites and energy (13.06 %), while decomposition, consumption and other activities account for 11.5 % (17). The rhizosphere region is the most studied microbiome among the three. It is a region where soil and its microbial communities are associated with the plant root zone. This region is considered as a hotspot for microbial communities which play a vital role in the growth and development of plants (18). Plant microbiomes play an important role in maintaining soil quality, thus increasing rice production and food security. This can be achieved by influencing the different stages of crop growth from sowing to maturity (19). For example, *Exiguobacterium* R2567 is a root microbiota that regulates tiller numbers in rice by producing Cyclo (Leu-Pro), which act similarly like plant's native hormone strigolactones (20). Understanding the interactions within host-microbiome systems and finding species along with their respective functionalities in a particular environment can prove to be a good strategy for getting enhanced rice yield, sustainability in farming practices and resilience under stress conditions (Table 1). Gene-related information in the plant microbiome, can be used in determining the microbial communities that support crop growth maximally and/or provide disease resistance (21). This gene-related research can aid in developing low fertilizer input responsive types that can grow in resource-limited settings while maintaining high productivity and sustainability.

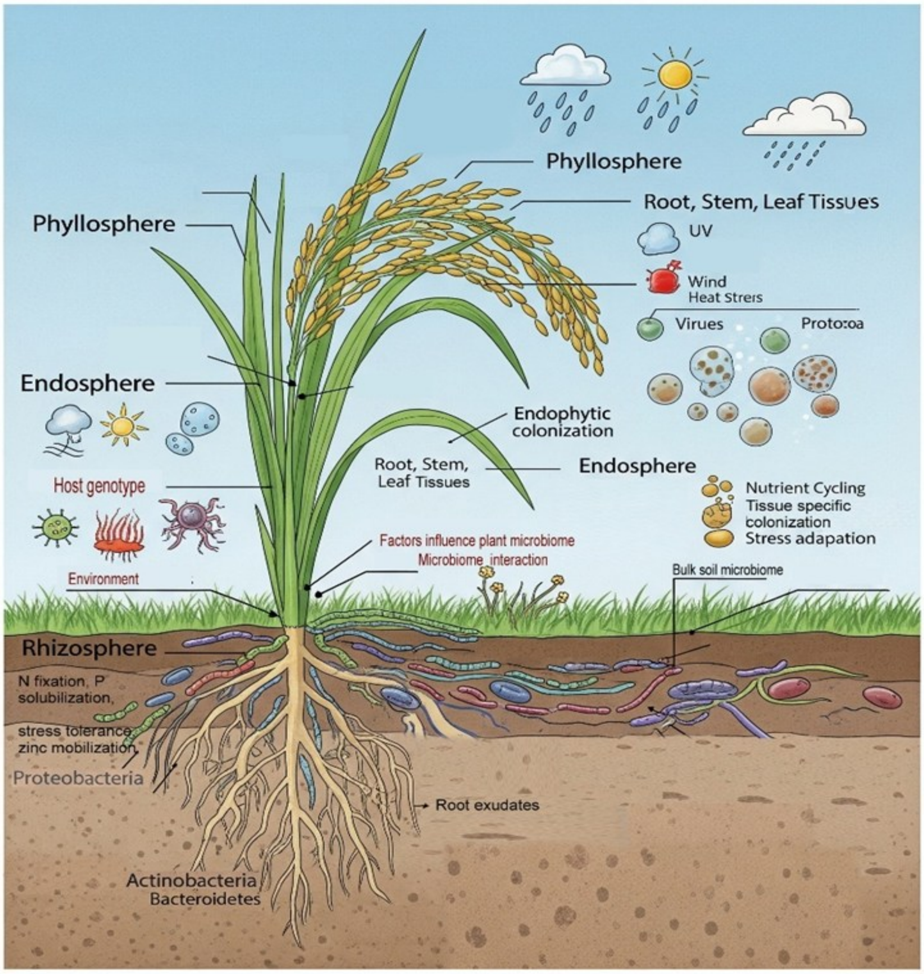

Fig. 2. Depiction of rice-microbiome interaction at various levels (phylloshphere, rhizosphere and endosphere).

Table 1. Microorganisms and their functions

Microorganism	Activity involved	Genotype/plant material	Reference
Phyllosphere			
Azorhizobium, Rhodopseudomonas. *Cyanobacteria*	Nitrogen fixation		(22)
Acinetobacter,firmicutes, Bacteroidetes, proteobacteria	Remediate of Methanol	*Oryza sativa*	(23)
Methylobacterium (leaf)	Plant growth-promoting metabolites	*Oryza sativa* landraces	(24)
Acinetobacter, Aureimonas, Pantoea and *Pseudomona*	Immunocompetence against blast disease.	*Oryza sativa* L. var. *japonica* cv. Xiushui 63	(25)
Pseudomonas sp. and *Bacillus*	siderophore production, inorganic phosphate solubilization, HCN production, Ammonia production, production IAA and cytokinin	Seven genotypes of rice ADT- 38, ADT-43, CR-1009, PB-1, PS-5, P-44 and PB-1509	(26)
Phaeosphaeria	Defence against pathogens by competing for resources. And production secondary metabolites	*Oryza rufipogan*	(6)
Curtobacterium pusillum	plant growth stimulation, enhancing the nutrient availability	*Oryza sativa* Koshihikari	(27)
Endophytes			
Bacteria *Pantoea anantis, Pantoea eucalypati* and *Pantoea vagans related strains*	Produce indole related compound and Plant growth promotion	*Oryza sativa* L. genotypes Arborio, Lamone, Arsenal and Ermes	(28)
Methanospirillum and *Methanobacterium*	Contributing to methane production and nutrient cycling	Various species	(29)
Desulfomonile and *Ruminiclostridium,*	nitrogen fixation and cellulose degradation	*Oryza officinalis*	(30)
Actobacillus, Acinetobacter and *Dechloromonas*	Phytopathogenic bacteria, nitrogen removal, biodegradation and iron oxidation		
Pseudomonadota (Proteobacteria) and *Actinomycetota (Actinobacteria)*	Heterosis and hybrid Vigor	Tianyouhuazhan (TFHZ), Zhongzheyou-H7 (ZYH7) and Huazheyou-261 (HZ261)	(31)
Rhizosphere			
Actinobacteria and *Chloroflexi*	Drought tolerance	*Oryza glaberrima, Oryza sativa*	(32)
Proteobacteria	de-nitrifier and nitrogen-fixing bacteria	*Oryza sativa* L. var. *japonica* cv. Xiushui 63	(33)
Azospira	de-nitrification and degradation of organic matter		
Rubrivivax	Plant growth-promoting and Cd-removing capacity	*Oryza sativa* L. var. *japonica* cv. Zhonghua 11	
Novosphingobium	Increase Plant development and productivity	*Oryza sativa*	(35)
Novosphingobium, gaiella, Nocardioides, Hydrogenophaga, lamia and *Geobactor*	Nutrition cycle support. Pathogen suppression. Nutrient assimilation. Enzyme production., Hormone secretion	*Oryza sativa*	(36)
Exiguobacterium R2567	Regulates tiller number by producing Cyclo (leu-Pro)	*Oryza sativa L. indica* and *Oryza sativa* L. *japonica*	(20)

Genetic factors influencing microbiome diversity in rice

The Mendelian and quantitative genetic variations contribute to microbial heritability. These factors play a crucial role in shaping the diversity of the microbiome associated with crops. Resilience and productivity are influenced by varying environmental conditions (37). It is very important to understand the genetic influences which can prove useful in developing rice varieties that utilize microbial interactions in a better way to get enhanced growth and stress tolerance. For example, the *OsPAL02* gene is a key player in the regulation of beneficial microbial communities in rice, linking plant genetics to microbiome diversity and functionality by influencing 4-hydroxycinnamic acid (4-HCA) production, which plays a significant role in shaping the rice phyllosphere microbiome and enhancing plant resilience against diseases by increasing the population of *Pseudomonadales* (38).

Additionally, understanding of genetic insights about microbiome interactions may provide the way for getting improved and reliable breeding strategies that can be used to develop varieties with better rice quality and more productivity. In this case, the *calcineurin B-like interacting protein kinase 2* gene, which plays a significant role in regulating root-associated microbiomes, could further enhance nutrient uptake and stress resilience in rice varieties (Table 2). This gene not only helps in nitrogen uptake but also strengthens its overall resistance to low-nitrogen stress conditions (39). Likewise, plants possess many genes that regulate the composition of chemicals released from their roots, known as root exudates. These exudates include chemical compounds like sugars, amino acids, organic acids and specialized secondary metabolites. These compounds not only act as a nutrient source for soil microbes but also function as biochemical signals that attract or repel specific microbial groups in the rhizosphere. This composition of root exudates is genetically controlled and different plant varieties release distinct chemical exudates (40,41).

The genetic differences directly influence the assembly and structure of the microbial communities that colonize the root zone. Interestingly, studies have shown that the microbial community is shaped early in the plant's development, guided by the specific exudate patterns produced (42). Furthermore, the VHA-A1 mutation in rice indirectly drives a change in the microbial ecosystem by altering rhizosphere conditions through root exudates, which can have downstream effects on plant health and productivity (43). The plant genetic factors determine exudate composition and also play a crucial role in controlling the existence of beneficial bacteria and fungi (40). Understanding and harnessing this genetic control over the root microbiome opens ways for microbiome-assisted crop improvement and sustainable agriculture (44). The genotype of the plant significantly influences the structural and functional variability of the microbiome found in the rhizosphere. The architecture of roots is crucial for the community present in the root zone. However, the establishment of the microbiome is not purely reliant on genetic factors but is also influenced by the environment and developmental stages of the host. In seeds, the microbiome influences the initial establishment of beneficial microbial communities, which are crucial for promoting plant health and productivity (45). This highlights the importance of integral approaches in rice breeding for yield stability (46). Additionally, microbiome diversity is not solely dependent upon the host genotype; rather, it is influenced by various environmental factors that shapes microbial communities. Hence it is difficult to understand plant-microbe interactions and the transmission of those microbes that play a role in comprehensive breeding strategies (47). It necessitates the formation of field plots for screening by increasing the microbiome diversity which are involved in functional properties. The process of rice domestication has significantly influenced the development of the contemporary microbiota community associated with cultivated rice varieties. To regain the complex and more diverse community of microbes through the incorporation of wild types into breeding programmes for more novel genes and superior varieties with chemical exudates profile (6,48,49). The microbial communities get affected in an environmental stress condition. For example, some orders of fungi, like *Pleosporales* and *Capnodiales*, increase during drought and can enhance the resilience of rice plants by improving nutrient acquisition and stress tolerance. Certain species such as *Ceratosphaeria* spp. and *Boudiera* spp., show a positive correlation with yield (37).

The genetic and proteomic components that govern microbial interactions can be manipulated; however, the specific microbial entities with which we seek to engage are a result of the environmental conditions surrounding the host organism or we must introduce them to the specific environment. However, the microbial community is heavily influenced by external factors like plant age and soil microbiome. A group of microbes is always linked to the plant microbiome and shows genetic variation, which means some numbers are influenced by the plant's genes. The interplay between genetic factors and soil microbiome plays a major role in shaping plant phenotype than the genetic factor alone was investigated (50). Diversity of microbiome is not shaped by a single genetic trait alone, but complex interplay of multiple factors like root architecture, signalling pathways and environmental stress conditions (51). This indicates that integration of both genetics and environmental needed in rice breeding programs. Understanding these interactions is essential for developing sustainable agricultural practices by reducing the chemical inputs while enhancing the resilience of rice crops by incorporating the microbes.

Table 2. Genes influencing microbial taxa and their roles in rice

Gene	Microbial taxa	Activity involved	Reference
kdpA; phoA	*Alcaligenes faecalis* *Metabacillus indicus*	Dual activity on phosphate and micronutrients; Solubilizes potassium via acid production	(52)
Pi.UreA, Pi.GlutN and *Pi.GlutS* *Pi.HexT5* and *Pi.PT*	*Piriformospora indica* *Azotobacter chroococcum*	Enhanced nitrogen transport; phosphorus mobilization and transport of phosphate by roots from the external rhizosphere	(53)
acdS; -	*Bacillus subtilis*; *Brucella haematophilum*; Multiple rhizospheric taxa	acdS gene encodes for the enzyme 1-aminocyclopropane-1-carboxylate (ACC) Increases water retention in soil; promotes drought resilience; Reduces ethylene via ACC deaminase; mitigates stress-induced inhibition.	(54)
-	*Azospirillum* sp.; *Bacillus* sp.; *Pseudomonas* sp.	Three microorganisms more relevant to assimilation of Fe, Mn and Zn which promotes the growth and productivity through enhance of metabolic and alleviation of micronutrient in adverse environments	(55)
multi-gene (via 16S rRNA sequencing)	Rhizospheric microbial consortia	Functional redundancy for PGP traits; improved plant growth like higher germination percent and increase in shoot length.	(56)
nifH + gcd + acdS	PGPR consortia (*Bacillus*, *Pseudomonas*, *Azospirillum*)	PGPR activities, example nitrogen fixation, phosphate solubilization, IAA production, ACC deaminase production and siderophore production.	(57)
OsAUX1 and *OsIAA1; OsYUCCA1, OsYUCCA3, OsIPT3* and *OsIPT5,*	*Streptomyces* sp.	Produces IAA and ACC deaminase; stimulate root hair proliferation, lateral root formation, early-stage nutrient uptake and involved auxin signalling.	(58)
OsPAD4, OsFMO1 and *OsEDS1*	endophytic *Bacillus* spp.	managing blast disease antibiosis and induced systemic resistance via the Jasmonic acid-dependent signalling pathway.	(59)
OsPR1.1, OsNPR1, OsPDF2.2, OsFMO, OsPAD4, OsCEBiP and *OsCERK1*	*Acinetobacter, Aureimonas, Pantoea* and *Pseudomonas*	Activation of those genes through conferred immunocompetence against blast disease by direct antibiosis and defense elicitation	(25)
Calcineurin B-like Interacting Protein Kinase 2(CIPK 2)	*Phenylobacterium* sp., *Rhizobium* sp., *Pleomorphomonas* sp., *Devosia* sp., *Sphingomonas* sp. and *Azospirillum* sp.	Enhancing nitrogen uptake in rice plants, particularly under nitrogen-deficient conditions. Overexpression of *OsCIPK2* with a root-specific promoter has been shown to improve rice growth and nitrogen uptake	(39)
VHA-A1	fungal taxa, particularly Ascomycota phylum and specific genera like *Cladosporium, Gibberella, Humicola* and *Penicillium.*	*VHA-A1* gene mutation in rice plants leads to an 'early senescence leaf' (*esl*) phenotype, which significantly alters plant physiological processes and, consequently, the composition of rhizosphere microbial communities	(43)

Investigation of host-microbe interaction on grain quality and nutritional traits

The complex interactions existing among different microbial communities and their contribution to the quality of grains and nutritional characteristics was studied by different groups (50). Recent advances in genomics have shown that beneficial microorganisms not only possess the capacity to enhance the nutritional profile of grains but also bring resilience against a range of abiotic stresses. Present studies demonstrated that microbial taxa could augment the bioavailability of essential micronutrients such as zinc and iron, which are critical for human health (60). Microbial interactions taking place within the complex environment of the rhizosphere play a crucial role in facilitating the solubilization of essential nutrients which significantly improve/enhance the ability of plants to absorb these vital elements. This ultimately results in an increase in the overall quality of grains with an improvement in their nutritional value. The accumulation of essential nutrients within cereal grains is modulated by the intricate interactions between host genetic factors and microbial communities. Studies have demonstrated that *NPF1.2* gene is supposed to facilitate the transport of nitrate while concurrently shaping the specific microbial taxa that contribute to nutrient acquisition (61).

Acknowledging this complex interaction is pivotal for elucidating the mechanisms underlying nutrient accumulation, which in turn enhances grain quality and elucidates the genetic determinants and microbial dynamics that arise from these genetic influences. Moreover, during stress conditions, microbial groups play a special role in regulating biochemical processes, which affect the quality of grain and changes in the diversity of microbes (50). The microbial communities not only assist in nutrient accumulation but in addition improve grain quality by decreasing heavy metal accumulation (4). Furthermore, the incorporation of zinc-solubilizing bacteria within rice cultivation practices increases nutrient availability and elevates overall grain quality (62). Thus, assembly of microbial communities is not random; rather, they are actively scrutinized by the plants to enhance nutrient acquisition (63). Recent improvements in system biology help in studying host-microbe interactions. By identifying and breeding for specific M-genes that promote beneficial microbial associations, it is possible to develop crops with enhanced nutritional value combined with various stress tolerance. For example, genome-wide association studies have identified genetic loci in maize that influence the composition of the rhizosphere microbiome, which for improving nutrient acquisition and disease resistance (64). Similarly, CRISPR-Cas9 editing has been used to engineer genes, therefore it enables the development of crops with enhanced microbial occurrence by editing the responsible genes for interaction, as result increased levels of nutrient uptake and overall fitness (65).

Understanding heritability in the microbiome context

The concept of heritability serves as an important criterion for understanding the genetic factors contributing to phenotypic variation within populations. Thus, heritability has expanded the understanding of host-associated microbiome. This led to the emergence of holobiont heritability, where both genetic and microbial components of a host are considered in shaping phenotypic traits. Understanding the heritability of the microbiome is increasingly recognized as crucial for applications in plant breeding, microbiome engineering and sustainable agriculture (66). Knowing the genetic factors influencing microbiome assembly will enhance crop resilience and for optimizing microbial interactions, as a result, productivity in a sustainable way. Factors influencing microbiome heritability due to host genetics and environmental conditions. Additionally, root architecture significantly shapes microbial communities through their exudates in the rhizosphere (67,68). Host genotype effects on microbiome composition are more in the rhizosphere than in other plant parts. This indicates that root architecture, influenced by genetic factors, plays a significant role in determining microbiome structure breeding for superior root architecture (root branching and root hairs) can enhance microbiome heritability, leading to improved plant health and productivity (42). Therefore, understanding the heritability of microbiomes can lead to the identification of genetic traits that promote beneficial microbial interactions.

Additionally, heritability estimates for plant-associated microbes are generally low, due to being influenced by both genetic and environmental factors, with randomness of environmental processes potentially masking genetic effects (69). Reliability of heritability estimates depends upon accurate data modelling and experimental design. The necessity for enhanced plant-microbe interaction arises from the fact that domesticated rice possesses adequate root architecture with respect to agronomic characteristics. Understanding the genetic control of such traits and their influence on microbial assembly, can enable breeders to target these traits to increase microbiome heritability (70). The concept of microbiomes as extended host phenotypes suggests that heritable microbes are consistently affected by host phenotype and fitness over time, potentially playing a role in host evolution and ecology (69). This understanding about the heritability microbiome is important for breeding programs to enhance agricultural sustainability and crop resilience.

Breeding strategies for optimizing rice-microbiome interactions

To optimize crop-microbe interactions through breeding techniques, efforts should be focused on enhancing genetic traits that promote beneficial microbial associations for the nutrient uptake and increased resilience against environmental stresses. The source for such novel traits can be found in related wild types and landraces of rice. The diverse genetic backgrounds and adaptations help in establishing a wild rice with a more diverse and complex network of microbes that are well-adapted to its natural environment (6,71). The incorporation of these traits through modern breeding techniques can help in achieving the desired interaction, which enhances the microbe's functionality and leads to higher productivity and resilience in a sustainable way. Conventional breeding show certain limitations in microbiome-mediated breeding, such as it is more time-consuming and show low selection (47). To overcome these issues, modern biotechnological tools are required and incorporation of these tools helps in the development of rice varieties that can get associated with beneficial microbial communities (72). To breed the extended genotype, integrating these native landraces into breeding initiatives can boost genetic diversity, which creates novel interactions due to their natural selection and absence of bottlenecks, resulting in better microbiome interactions and increased resilience to the environment (73).

Technique of metagenomics is employed to analyse the genetic material of entire microbials or particular microorganism from communities present in various environments. Conventional breeding takes time and is not reliable due to errors; therefore, use of integrated system biology and biotechnological tools reduce the time required and increase the reliability of incorporating genes responsible for beneficial microbial interactions (74,75). Use of advanced tools can significantly enhance the efficiency of breeding programs, allowing for the faster development of rice varieties and microbiome mediated low input responsive variety, which holds the potential for enhance crop performance, especially in nutrient-poor environments by leveraging plant-microbe interactions, which is important in nutrient deficient and minimal external inputs like synthetic fertilizers and pesticides (76). A previous study in indica and japonica-enriched bacterial consortia to explore nitrogen uptake in rice under restrict N sources and identified *NRT1.1B* gene as key regulator in recruiting N-metabolizing microbiota and this highlights the role of host genotype-microbiome interaction promotes nitrogen use efficiency for developing low input response varieties (77) (Fig. 3). For more accurate results, Genome -Scale Metabolic models (GEMs) assist in clarifying microbial functions by outlining metabolic reactions and fluxes, allowing researchers to forecast which microbial characteristics (78). These advances guide rice breeding programmes to more precisely host traits, which ultimately leads to improved relationships. In addition, the eco-evolutionary model provides an understanding of how rice genotypes interact with their microbiomes over time (79). Here, not only do genetic factors play a major role, but the environment does as well, so we need more reconfirmation in different environments. To counter this flaw, we need a newer model like microbiome enable genomic selection, which uses SNPs from plants and connects data from the associated microbiome framework, revealing improved predictive precision for trait selection in maize. Implementing similar genomic selection techniques in rice breeding may yield more accurate breeding results, assuring that chosen varieties are ideally adapted to environmental conditions and challenges (41). From this, we can also find specific environments environment positively correlate with specific beneficial microbe communities. Once the genes or genetic factors responsible for the interaction are known, gene editing tools like CRISPR/Cas9 technology can be employed to precisely edit genes associated with beneficial microbial interactions, enhancing rice varieties resilience and productivity in diverse environmental conditions. By the combination of those technologies and incorporating those in the breeding field will aid in the development of more resilient rice varieties with complex and diverse interactions with microbial communities, as this will ultimately help in achieving sustainability in agriculture.

Multi-omics integration for understanding host-microbe interactions

The use of advanced techniques has changed our knowledge about microbial communities and their interaction with the host. Metagenomics, metatranscriptomics and metabolomics offer complex but complementary points of view on the microbial world, especially on plant health, soil ecology and sustainable agriculture. Metagenomics serves as a fundamental tool in microbiome research by enabling the investigation of the entire genetic material present within environmental samples, without

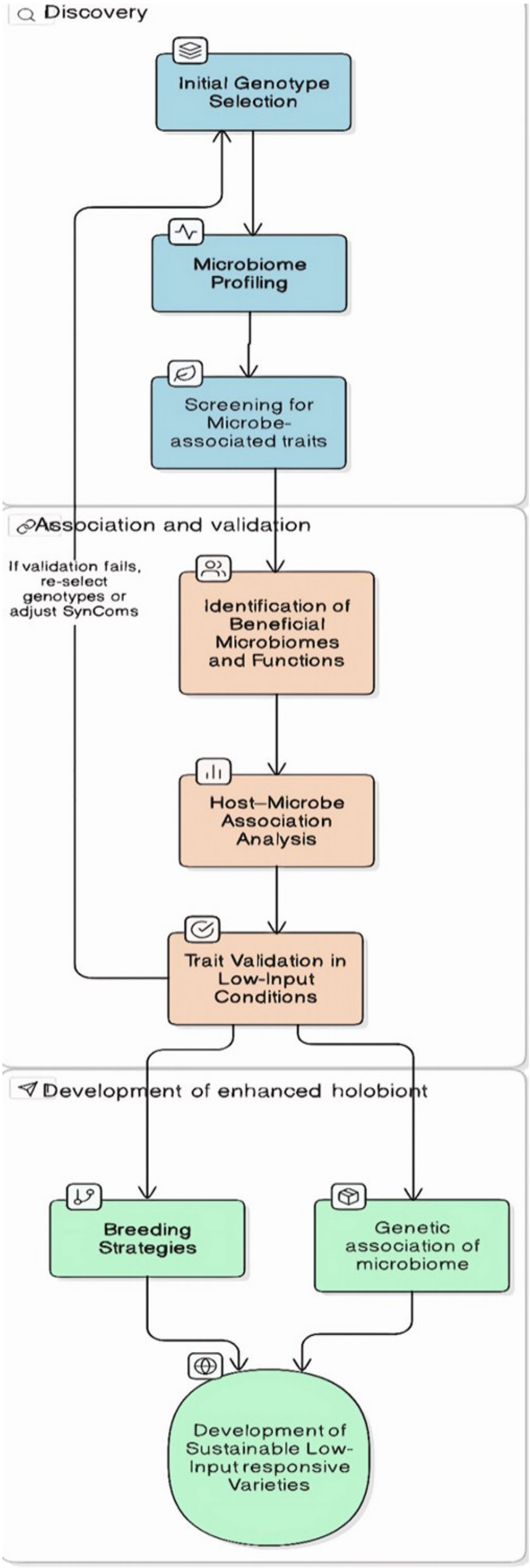

Fig. 3. Flow chart showing steps involved in development of sustainable low input responsive varieties.

the need for culturing individual organisms. In a previous study conducted on the rice phyllosphere among 166 identified bacterial species, 121 were found to be novel species (80). High-throughput sequencing technologies allow for the reconstruction of microbial community profiles from soil, rhizospheres and plant tissues (27). These insights are instrumental in identifying both the diversity and abundance of microorganisms, including those with Plant Growth-Promoting (PGP) traits. Some previous studies have highlighted the power of metagenomics to uncover microbial taxa involved in nutrient cycling, phytohormone production and stress resistance functions that are critical for developing microbiome-based strategies for sustainable agriculture (63,79).

However, the presence of a gene does not necessarily mean that it will be expressed or active. To address this gap, meta -transcriptomics is used to capture the active state of microbial communities by sequencing total messenger RNA (mRNA). This approach provides a snapshot of genes being actively transcribed at the time or time of sampling, giving a real-time insight into microbial functionality under specific environmental or biological conditions (81). For example, a study conducted in switchgrass indicates variation (during the late season) in expression of microbial genes, particularly upregulation of GcpE and LytB genes. As a result, isoprene biosynthesis pathway increases and it is known to act as signalling molecule in stress response (82), in another similar study conducted on contribution of rhizosphere microbiome in rice salt tolerance (83). Techniques such as illumina sequencing, after rRNA depletion and reverse transcription, allow researchers to trace gene expression dynamics linked to plant-microbe interactions. Functional annotation through tools like Bowtie2, KEGG and Gene Ontology enables the mapping of microbial contributions to metabolic pathways, which can influence traits such as disease resistance, nutrient uptake and abiotic stress tolerance in plants (84), which will help in later breeding programmes and microbiome engineering. Nevertheless, technical hurdles like mRNA instability and the ratio of rRNA in total RNA extractions remain challenges that need refinement (85,86). To complete the interaction view, metabolomics is applied to study the chemical fingerprints left by microbial and plant metabolism.

This approach identifies and quantifies small molecules (metabolites) in plant tissues or rhizosphere through root exudates, reflecting the ultimate output of gene expression and enzyme activity. Metabolomics is thus considered a phenotypic endpoint of biological processes and is pivotal for understanding how microbiota influence plant secondary metabolism, stress responses and growth (87,88). For example, a previous study used metabolomics to analyse root tissues of *Aconitum vilmorinianum*, identifying unique alkaloidal metabolites linked to microbial functions (81). Moreover, integrative approaches combining metabolomics with predictive tools like PICRUSt2 and FUNGuild have revealed how rhizosphere microbes modulate amino acid metabolism pathways, influencing bioactive compound synthesis. For example- the *GmAMT2.1/2.2* gene from soybean encodes ammonium transporters in roots, which also mitigate cadmium exposure by upregulating the gene under cadmium stress and causing significant changes in the microbial community due to changes in root exudate composition resulting from those genes (89). The incorporation of multi-omics facilitates significant insights about the metabolites that steer microbial communities, their functions and the genes responsible for metabolite production (Fig. 4). This information will help integrate those genes into breeding programs, aiding in the development of rice varieties that not only thrive in diverse environmental conditions but also contribute to sustainable agricultural practices, enhancing food security and environmental health (65).

Fig. 4. Integrative multi-omics for microbiome-assisted rice improvement.

Challenges and future directions in microbiome-driven rice sustainability research

In consideration of the increasing knowledge regarding the crucial role of the rice microbiome for its sustainability, a multitude of challenges including likely limited resolution of microbial communities, lack of standardized phenotyping and data integration are in the genetic implementation microbes through breeding programmes and their complexity and their constant changes in during the lifecycle of host that need to be addressed. These include understanding the interactions between microbiome-encoded genetic factors and host traits, as well as the complexities of microbiome transmission during breeding processes (90). The major area of research uses sole 16S rRNA sequencing to study microbial communities, but this sequencing has its disadvantages, such as being applicable only to bacterial communities, its resolution power and its inability to draw conclusions about the functions or accurately identify the species present (27). This disadvantage reflects in the plant microbiome due to its failure to address the other microorganisms present alongside the identified microbes, which leads to the neglect of those microorganisms' influence and interactions with the host and other microbes in the community. To effectively address these diverse microbial assemblages (microbiome), it is costly to utilize distinct primer sets and specific amplification conditions, using 16S rRNA for bacterial identification and ITS for fungal analysis in this investigation. The standardization of the steps may require a process of troubleshooting and validation of errors, thereby cost will more at initial implementation (91).

In addition, the resolution of microbial communities should increase using next-generation sequencing for more accuracy. Estimating microbiome heritability is complex due to the use of compositional data, which can lead to spurious correlations and biased estimates. This issue is particularly pronounced for dominant taxa and when large sample sizes are involved (92). Phenotyping the microbiome in host-associated systems presents a variety of challenges arising from both biological complexities, such as host traits, environmental factors and interactions with other microbes, as well as technical limitations.

The task of isolating the specific contributions of microbiome-encoded genetic factors have challenges like confounding effects (difficulty to separate direct genetic effect from microbiome-mediated ones), insufficient sample size and weak host-microbe association. In addition to that, the variability and low heritability of microbial communities to phenotypes also contributes to the problem. Such variability makes it difficult to set a standard microbial diversity in ecology (70). Although superior plant varieties can be developed with better root exudates and traits that boost nutrient uptake for microbial interaction. In contrast, the microbes attracted through those exudates will differ depending on the environment, making the implication more difficult under different conditions. Understanding these dynamics will be crucial for developing effective microbiome-based breeding strategies. Furthermore, it will be difficult for to study phyllosphere interaction because of the low biomass of microbes to analyse and the presence of environmental inhibitors.

Addressing these challenges will require innovative sampling techniques and advanced analytical methods to accurately capture and analyse the microbial diversity present in varying environments and require more time of research to develop reliable methodologies for assessing microbiome interactions with plant traits across diverse conditions (93). A major difficulty or challenge is that the genetic factors are already present, but microbes do not dominate in specific places or environments. This leads the research to restrict to area-specific studies and the colonization of bacteria is good idea but has their disadvantage like presence of these inoculated microbes interference from naturally occurring environmental strains makes it difficult to directly link yield improvements to the inoculated microbes (24). In that case, we can go for synthetic microbial communities (SynComs) inoculation, which are designed to study interactions between microbes and their hosts in a controlled environment, limiting external factors. However, that is also challenging because there is not full understanding of balancing microbial diversity with functional specificity (94).

The final challenge posed by multi-omics microbiome data and their validation is due to their significant complexity of the involved datasets and limited model for analysis. A key issue is the high dimensionality of the data, where each omics layer (such as taxonomic profiles, pathway-level data and metabolomics), contains many features that are often highly variable. It is essential to filter out rare or low abundance features to ensure that the following analyses are strong. This issue is made worse by different processing methods of different omics, which can introduce biases or technical artifacts that further complicate data interpretation. Furthermore, large-scale data will also lead to false discovery of candidate genes associated with specific traits, complicating the identification of reliable genetic markers for breeding programs (69,74). For instance, the *GmAMT2.1/2.2* gene in soybean plays a crucial role in mitigating external cadmium toxicity and its effects on microbial communities; however, the full potential of this gene has not been fully explored (89). Furthermore, biological validation requires extensive data from independent cohorts or experimental setups that have comparable multi-omics measurements. Variations in sample collection, processing and presence of various types of microbes present across studies result in differences making the comparison more difficult. As noted, even with robust statistical pipelines, there is often a lack of systematic mapping between multi-omics interactions and known biological pathways or disease mechanisms (74).

The sustainability of rice production is under increasing threat from environmental stresses and climate change patterns. Limiting factors in rice production under present scenarios have been discussed. Microbiome-driven research offers promising solutions to enhance rice cultivation. However, this also faces challenges that need to be addressed. Firstly, to effectively harness breeding programmes and microbiome engineering for rice improvement, it is crucial to identify Quantitative Trait Loci (QTLs) associated with beneficial microbial interactions. Current state of microbiome-QTL platforms demonstrates promising integration of plant quantitative genetics with high-resolution microbial genomic data, but considerable development is yet to be achieved (95). But we need more and refined resolution of microbial quantification to accurately map these interactions.

Enhancing the precision of microbiome-QTL platforms will facilitate the identification of specific genetic loci that influence microbial community dynamics in rice and precision can be achieved with the assistance of next-generation sequencing (96). Before the practical use of microbiome-mediated technologies in breeding programs, it is essential to validate these QTLs across diverse environmental conditions to ensure their stability and applicability in real-world scenarios. Additionally, for accurate validation, the implementation of conceptual and analytical tools, such as network mapping in microbiome research, can provide insights into the interactions between plant genotypes and, importantly, between the microbes. This will help in countering the complex interactions and their heritability (97). These new models should have to more reliable and accurate for complexity. Additionally, it holds the reliability for future research. More to add, understanding that complex interplay within and among biological systems is increasingly needed in microbiome research (74, 98).

In the future, this improvement will produce a large amount of data and for that, we need a proper model to interpret and manage this information effectively; otherwise, it will lead to false interpretations (92). SynComs can enhance our understanding of these interactions by providing a controlled environment to study the effects of specific microbial combinations on rice health and productivity. Moreover, this artificial communities have their drawback when comes to field level on replicating the complexity of natural microbiome and this challenge requires further research to ensure that findings from SynComs studies can be effectively applied in real-time (99). Integrated approaches of microbial ecology this can lead to improved agricultural practices and sustainability.

Conclusion

Microbiome associations in wild relatives of rice and landraces is attributed by host genetic factors and their adaptive environments. The coordinated genetic regulations enable the rice to attain growth and development. Transfer of microbiome associated traits through breeding strategies should involve recent techniques and methods for developing more resilient rice variety. Low input response rice varieties will have positive impact on rice growing environments due to reduced usage of chemical inputs for cultivation. Improving the microbiome diversity in rice environment will have long lasting effect on soil fertility and sustainability. To achieve the development of superior microbiome mediated varieties, efforts are being undertaken to characterize the wild relatives and land races for microbiome association on genetic, metabolomic and phenotypic levels. Breeding efforts should be focused on rice geographical region by mapping the climate and soil parameters for developing region-specific low input response rice varieties which have specific and abundant microbiome. Microbiome mediated crop improvement is still in conceptive stages but can prove as an efficient and effective method to overcome the negative impacts of high chemical inputs usage in the near future.

Acknowledgements

The authors are grateful to the Anbil Dharmaingam Agricultural college and Research Institute (ADAC&RI), Trichy and Tamil Nadu Rice Research Institute, Aduthurai for providing the necessary resources and academic environment to carry out this review work. We would like to express our sincere thanks to other scientist and faculty members of the Department of Genetics and Plant Breeding, for their valuable support, guidance and encouragement throughout the preparation of this article.

Authors' contributions

The first draft of the manuscript was written by PP, SK, AR, PR[1] and RP. PR[2] assisted with critical revisions and formatting. DM provided guidance for overall correction and improvement in writing. All authors read and approved the final manuscript. [PR[1] stands for Parthasarathi R and PR[2] stands for Pushpa R].

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interests to declare.

Ethical issues: None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Gemini AI/ Google for assisting in the initial drafting of illustrations used in this review. The final figures were reviewed and edited by the authors. After using this tool/service, the authors reviewed and edited the content as needed and takes full responsibility for the content of the publication.

References

1. FAO. World food and agriculture - statistical yearbook 2023. Rome; 2023
2. Zhao C, Liu G, Chen Y, Jiang Y, Shi Y, Zhao L, et al. Excessive nitrogen application leads to lower rice yield and grain quality by inhibiting the grain filling of inferior grains. Agriculture. 2022;12(7):962. https://doi.org/10.3390/agriculture12070962
3. Adhikari A, Kwon EH, Khan MA, Shaffique S, Kang SM, Lee IJ. Enhanced use of chemical fertilizers and mitigation of heavy metal toxicity using biochar and the soil fungus *Bipolaris maydis* AF7 in rice: genomic and metabolomic perspectives. Ecotoxicol Environ Saf. 2024;271:115938. https://doi.org/10.1016/j.ecoenv.2024.115938
4. Du F, Yang Z, Liu P, Wang L. Accumulation, translocation and assessment of heavy metals in the soil-rice systems near a mine-impacted region. Environ Sci Pollut Res Int. 2018;25(32):32221-30. https://doi.org/10.1007/s11356-018-3184-7
5. Zhong Y, Hu J, Xia Q, Zhang S, Li X, Pan X, et al. Soil microbial mechanisms promoting ultrahigh rice yield. Soil Biol Biochem. 2020;143:107741. https://doi.org/10.1016/j.soilbio.2020.107741
6. Yin Y, Wang YF, Cui HL, Zhou R, Li L, Duan GL, et al. Distinctive structure and assembly of phyllosphere microbial communities between wild and cultivated rice. Microbiol Spectr. 2023;11 (1):e04371-22. https://doi.org/10.1128/spectrum.04371-22
7. Nicotra D, Ghadamgahi F, Ghosh S, Anzalone A, Dimaria G, Mosca A, et al. Genomic insights and biocontrol potential of ten bacterial strains from the tomato core microbiome. Front Plant Sci. 2024;15:1437947. https://doi.org/10.3389/fpls.2024.1437947

8. Walitang DI, Roy Choudhury A, Subramanian P, Lee Y, Choi G, Cho K, et al. Microbe-responsive proteomes during plant-microbe interactions between rice genotypes and the multifunctional *Methylobacterium oryzae* CBMB20. Rice. 2023;16(1):23. https://doi.org/10.1186/s12284-023-00639-y
9. Wang Z, Song Y. Toward understanding the genetic bases underlying plant-mediated "cry for help" to the microbiota. iMeta. 2022;1(1):e8. https://doi.org/10.1002/imt2.8
10. Barnes CJ, Bahram M, Nicolaisen M, Gilbert MTP, Vestergård M. Microbiome selection and evolution within wild and domesticated plants. Trends Microbiol. 2025;33(4):447-58. https://doi.org/10.1016/j.tim.2024.11.011
11. Singh A, Kumar M, Chakdar H, Pandiyan K, Kumar SC, Zeyad MT, et al. Influence of host genotype in establishing root associated microbiome of indica rice cultivars for plant growth promotion. Front Microbiol. 2022;13:1033158. https://doi.org/10.3389/fmicb.2022.1033158
12. Michl K, Berg G, Cernava T. The microbiome of cereal plants: the current state of knowledge and the potential for future applications. Environ Microbiome. 2023;18(1):28. https://doi.org/10.1186/s40793-023-00484-y
13. Orozco-Mosqueda M del C, Rocha-Granados M del C, Glick BR, Santoyo G. Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. Microbiol Res. 2018;208:25-31. https://doi.org/10.1016/j.micres.2018.01.005
14. Zhao J, Yu X, Zhang C, Hou L, Wu N, Zhang W, et al. Harnessing microbial interactions with rice: strategies for abiotic stress alleviation in the face of environmental challenges and climate change. Science of The Total Environment. 2024;912:168847. https://doi.org/10.1016/j.scitotenv.2023.168847
15. Bashir I, War AF, Rafiq I, Reshi ZA, Rashid I, Shouche YS. Phyllosphere microbiome: diversity and functions. Microbiol Res. 2022;254:126888. https://doi.org/10.1016/j.micres.2021.126888
16. Vorholt JA. Microbial life in the phyllosphere. Nat Rev Microbiol. 2012;10(12):828-40. https://doi.org/10.1038/nrmicro2910
17. Tran DM, Nguyen TH. Rice (*Oryza sativa* L.) cultivated in the central highlands of Vietnam: dataset on the endophytic microbiome. Data Brief. 2023;50:109551. https://doi.org/10.1016/j.dib.2023.109551
18. Zhang J, Cook J, Nearing JT, Zhang J, Raudonis R, Glick BR, et al. Harnessing the plant microbiome to promote the growth of agricultural crops. Microbiol Res. 2021;245:126690. https://doi.org/10.1016/j.micres.2020.126690
19. Doni F, Suhaimi NSM, Mispan MS, Fathurrahman F, Marzuki BM, Kusmoro J, et al. Microbial contributions for rice production: from conventional crop management to the use of 'omics' technologies. Int J Mol Sci. 2022;23(2):737. https://doi.org/10.3390/ijms23020737
20. Zhang J, Wang B, Xu H, Liu W, Yu J, Wang Q, et al. Root microbiota regulates tiller number in rice. Cell. 2025;188(12):3152-66.e16. https://doi.org/10.1016/j.cell.2025.03.033
21. Deschênes T, Tohoundjona FWE, Plante PL, Di Marzo V, Raymond F. Gene-based microbiome representation enhances host phenotype classification. mSystems. 2023;8(4):e00531-23. https://doi.org/10.1128/msystems.00531-23
22. Venkatachalam S, Ranjan K, Prasanna R, Ramakrishnan B, Thapa S, Kanchan A. Diversity and functional traits of culturable microbiome members, including cyanobacteria in the rice phyllosphere. Plant Biol (Stuttg). 2016;18(4):627-37. https://doi.org/10.1111/plb.12441
23. Knief C, Delmotte N, Chaffron S, Stark M, Innerebner G, Wassmann R, et al. Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. ISME J. 2012;6(7):1378-90. https://doi.org/10.1038/ismej.2011.192
24. Sanjenbam P, Shivaprasad PV, Agashe D. Impact of phyllosphere *Methylobacterium* on host rice landraces. Microbiol Spectr. 2022;10(4):e00810-22. https://doi.org/10.1128/spectrum.00810-22
25. Sahu KP, Kumar A, Sakthivel K, Reddy B, Kumar M, Patel A, et al. Deciphering core phyllomicrobiome assemblage on rice genotypes grown in contrasting agroclimatic zones: implications for phyllomicrobiome engineering against blast disease. Environ Microbiome. 2022;17(1):28. https://doi.org/10.1186/s40793-022-00421-5
26. Thapa S, Prasanna R, Ranjan K, Velmourougane K, Ramakrishnan B. Nutrients and host attributes modulate the abundance and functional traits of phyllosphere microbiome in rice. Microbiol Res. 2017;204:55-64. https://doi.org/10.1016/j.micres.2017.07.007
27. Masuda S, Gan P, Kiguchi Y, Anda M, Sasaki K, Shibata A, et al. Uncovering microbiomes of the rice phyllosphere using long-read metagenomic sequencing. Commun Biol. 2024;7(1):357. https://doi.org/10.1038/s42003-024-05998-w
28. Ahumada GD, Gómez-Álvarez EM, Dell'Acqua M, Bertani I, Venturi V, Perata P, et al. Bacterial endophytes contribute to rice seedling establishment under submergence. Front Plant Sci. 2022;13:908349. https://doi.org/10.3389/fpls.2022.908349
29. Edwards J, Johnson C, Santos-Medellín C, Lurie E, Podishetty NK, Bhatnagar S, et al. Structure, variation and assembly of the root-associated microbiomes of rice. Proc Natl Acad Sci U S A. 2015;112(8):E911-20. https://doi.org/10.1073/pnas.1414592112
30. Tian Q, Gong Y, Liu S, Ji M, Tang R, Kong D, et al. Endophytic bacterial communities in wild rice (*Oryza officinalis*) and their plant growth-promoting effects on perennial rice. Front Plant Sci. 2023;14:1184489. https://doi.org/10.3389/fpls.2023.1184489
31. Liu Y, Zhao K, Stirling E, Wang X, Gao Z, Ma B, et al. Heterosis of endophytic microbiomes in hybrid rice varieties improves seed germination. mSystems. 2024;9(5):e00004-24. https://doi.org/10.1128/msystems.00004-24
32. Santos-Medellín C, Edwards J, Liechty Z, Nguyen B, Sundaresan V. Drought stress results in a compartment-specific restructuring of the rice root-associated microbiomes. mBio. 2017;8(4):e00764-17. https://doi.org/10.1128/mBio.00764-17
33. Qian H, Zhu Y, Chen S, Jin Y, Lavoie M, Ke M, et al. Interacting effect of diclofop-methyl on the rice rhizosphere microbiome and denitrification. Pestic Biochem Physiol. 2018;146:90-6. https://doi.org/10.1016/j.pestbp.2018.03.002
34. Li K, Wang C, Ow DW. Root microbiome changes associated with cadmium exposure and/or overexpression of a transgene that reduces Cd content in rice. Ecotoxicol Environ Saf. 2022;237:113530. https://doi.org/10.1016/j.ecoenv.2022.113530
35. Chinta YD, Araki H. Responses of bulk and rhizosphere soil microbiomes to different cover crop inputs and their connection and contribution to soil fertility and plant growth. Pedobiologia. 2023;101:150907. https://doi.org/10.1016/j.pedobi.2023.150907
36. Liu T, Wei J, Yang J, Wang H, Wu B, He P, et al. Polyaspartic acid facilitated rice production by reshaping soil microbiome. Appl Soil Ecol. 2023;191:105056. https://doi.org/10.1016/j.apsoil.2023.105056
37. Andreo-Jimenez B, te Beest DE, Kruijer W, Vannier N, Kadam NN, Melandri G, et al. Genetic mapping of the root mycobiota in rice and its role in drought tolerance. Rice. 2023;16(1):26. https://doi.org/10.1186/s12284-023-00641-4
38. Su P, Kang H, Peng Q, Wicaksono WA, Berg G, Liu Z, et al. Microbiome homeostasis on rice leaves is regulated by a precursor molecule of lignin biosynthesis. Nat Commun. 2024;15(1):23. https://doi.org/10.1038/s41467-023-44335-3
39. Chen M, Feng S, Lv H, Wang Z, Zeng Y, Shao C, et al. OsCIPK2 mediated rice root microorganisms and metabolites to improve plant nitrogen uptake. BMC Plant Biol. 2024;24(1):285. https://doi.org/10.1186/s12870-024-04982-0
40. Afridi MS, Kumar A, Javed MA, Dubey A, de Medeiros FHV, Santoyo G. Harnessing root exudates for plant microbiome engineering and stress resistance in plants. Microbiol Res. 2024;279:127564. https://doi.org/10.1016/j.micres.2023.127564
41. Tong Y, Zheng X, Hu Y, Wu J, Liu H, Deng Y, et al. Root exudate-

mediated plant-microbiome interactions determine plant health during disease infection. Agric Ecosyst Environ. 2024;370:109056. https://doi.org/10.1016/j.agee.2024.109056

42. Alahmad A, Harir M, Fochesato S, Tulumello J, Walker A, Barakat M, et al. Unraveling the interplay between root exudates, microbiota and rhizosheath formation in pearl millet. Microbiome. 2024;12(1):1. https://doi.org/10.1186/s40168-023-01727-3

43. Letuma P, Arafat Y, Waqas M, Lin F, Lin W, Zhang Y, et al. Gene mutation associated with esl mediates shifts on fungal community composition in rhizosphere soil of rice at grain-filling stage. Sci Rep. 2018;8(1):17521. https://doi.org/10.1038/s41598-018-35578-y

44. Afridi MS, Javed MA, Ali S, de Medeiros FHV, Ali B, Salam A, et al. New opportunities in plant microbiome engineering for increasing agricultural sustainability under stressful conditions. Front Plant Sci. 2022;13:899464. https://doi.org/10.3389/fpls.2022.899464

45. Kumar A, Solanki MK, Wang Z, Solanki AC, Singh VK, Divvela PK. Revealing the seed microbiome: navigating sequencing tools, microbial assembly and functions to amplify plant fitness. Microbiol Res. 2024;279:127549. https://doi.org/10.1016/j.micres.2023.127549

46. Quiza L, Tremblay J, Pagé AP, Greer CW, Pozniak CJ, Li R, et al. The effect of wheat genotype on the microbiome is more evident in roots and varies through time. ISME Commun. 2023;3(1):32. https://doi.org/10.1038/s43705-023-00238-4

47. Michl K, David C, Dumont B, Mårtensson LMD, Rasche F, Berg G, et al. Determining the footprint of breeding in the seed microbiome of a perennial cereal. Environ Microbiome. 2024;19(1):40. https://doi.org/10.1186/s40793-024-00584-3

48. Banik A, Mukhopadhaya SK, Dangar TK. Characterization of N2-fixing plant growth promoting endophytic and epiphytic bacterial community of Indian cultivated and wild rice (*Oryza* spp.) genotypes. Planta. 2015;243(3):799-812. https://doi.org/10.1007/s00425-015-2444-8

49. Fornasiero A, Wing RA, Ronald P. Rice domestication. Curr Biol. 2022;32(1):R20-4. https://doi.org/10.1016/j.cub.2021.11.025

50. Jiang M, Wang Z, Li X, Liu S, Song F, Liu F. Relationship between endophytic microbial diversity and grain quality in wheat exposed to multi-generational CO2 elevation. Sci Total Environ. 2021;776:146029. https://doi.org/10.1016/j.scitotenv.2021.146029

51. Bamba M, Akyol TY, Azuma Y, Quilbe J, Andersen SU, Sato S. Synergistic effects of plant genotype and soil microbiome on growth in *Lotus japonicus*. FEMS Microbiol Ecol. 2024;100(5):fiae056. https://doi.org/10.1093/femsec/fiae056

52. Fatema K, Mahmud NU, Gupta DR, Siddiqui MN, Sakif TI, Sarker A, et al. Enhancing rice growth and yield with weed endophytic bacteria *Alcaligenes faecalis* and *Metabacillus indicus* under reduced chemical fertilization. PLoS One. 2024;19(5):e0296547. https://doi.org/10.1371/journal.pone.0296547

53. Bandyopadhyay P, Yadav BG, Kumar SG, Kumar R, Kogel KH, Kumar S. *Piriformospora indica* and *Azotobacter chroococcum* consortium facilitates higher acquisition of N, P with improved carbon allocation and enhanced plant growth in *Oryza sativa*. J Fungi (Basel). 2022;8(5):453. https://doi.org/10.3390/jof8050453

54. Mahreen N, Yasmin S, Asif M, Yahya M, Ejaz K, Mehboob-Ur-Rahman, et al. Mitigation of water scarcity with sustained growth of rice by plant growth promoting bacteria. Front Plant Sci. 2023;14:1081537. https://doi.org/10.3389/fpls.2023.1081537

55. Pico Y, Paz R, Rayo S. Optimizing iron, manganese and zinc fertilization in rice (*Oryza sativa* L.) through *Bacillus*, *Pseudomonas* and *Azospirillum* bacteria. Rev Fac Cienc Básicas. 2024;18:83-101. https://doi.org/10.18359/rfcb.7055

56. Srija A, Latha PC, Tejashree M, Reddy K, Triveni S, Bandeppa S, et al. Identification and in vitro evaluation of environmental stress resilient plant growth promoting rhizobacterial consortia for rice (*Oryza sativa* L.). Int J Environ Clim Change. 2022;12(11):3340-54. https://doi.org/10.9734/ijecc/2022/v12i111384

57. Thamvithayakorn P, Phosri C, Robinson-Boyer L, Limnonthakul P, Doonan JH, Suwannasai N. The synergistic impact of a novel plant growth-promoting rhizobacterial consortium and *Ascophyllum nodosum* seaweed extract on rhizosphere microbiome dynamics and growth enhancement in *Oryza sativa* L. RD79. Agronomy. 2024;14(11):2698. https://doi.org/10.3390/agronomy14112698

58. Thenappan DP, Pandey R, Hada A, Jaiswal DK, Chinnusamy V, Bhattacharya R, et al. Physiological basis of plant growth promotion in rice by rhizosphere and endosphere associated *Streptomyces* isolates from India. Rice. 2024;17(1):60. https://doi.org/10.1186/s12284-024-00732-w

59. Velmurugan S, Ashajyothi M, Charishma K, Kumar S, Balamurugan A, Javed M, et al. Enhancing defense against rice blast disease: unveiling the role of leaf endophytic firmicutes in antifungal antibiosis and induced systemic resistance. Microb Pathog. 2023;184:106326. https://doi.org/10.1016/j.micpath.2023.106326

60. Singh DP, Singh V, Gupta VK, Shukla R, Prabha R, Sarma BK, et al. Microbial inoculation in rice regulates antioxidative reactions and defense related genes to mitigate drought stress. Sci Rep. 2020;10(1):4818. https://doi.org/10.1038/s41598-020-61140-w

61. Wang Y, Wang X, Sun S, Jin C, Su J, Wei J, et al. GWAS, MWAS and mGWAS provide insights into precision agriculture based on genotype-dependent microbial effects in foxtail millet. Nat Commun. 2022;13(1):5913. https://doi.org/10.1038/s41467-022-33238-4

62. Zeb H, Hussain A, Naveed M, Ditta A, Ahmad S, Jamshaid MU, et al. Compost enriched with ZnO and Zn-solubilising bacteria improves yield and Zn-fortification in flooded rice. Ital J Agron. 2018;13(4):310-6. https://doi.org/10.4081/ija.2018.1295

63. Camargo AP, de Souza RSC, Jose J, Gerhardt IR, Dante RA, Mukherjee S, et al. Plant microbiomes harbor potential to promote nutrient turnover in impoverished substrates of a Brazilian biodiversity hotspot. ISME J. 2023;17(3):354-70. https://doi.org/10.1038/s41396-022-01345-1

64. Escudero-Martinez C, Coulter M, Alegria Terrazas R, Foito A, Kapadia R, Pietrangelo L, et al. Identifying plant genes shaping microbiota composition in the barley rhizosphere. Nat Commun. 2022;13(1):3443. https://doi.org/10.1038/s41467-022-31022-y

65. Cernava T. Coming of age for microbiome gene breeding in plants. Nat Commun. 2024;15(1):6623. https://doi.org/10.1038/s41467-024-50700-7

66. Zhang X, Ma YN, Wang X, Liao K, He S, Zhao X, et al. Dynamics of rice microbiomes reveal core vertically transmitted seed endophytes. Microbiome. 2022;10(1):216. https://doi.org/10.1186/s40168-022-01422-9

67. Salas-González I, Reyt G, Flis P, Custódio V, Gopaulchan D, Bakhoum N, et al. Coordination between microbiota and root endodermis supports plant mineral nutrient homeostasis. Science. 2021;371(6525):eabd0695. https://doi.org/10.1126/science.abd0695

68. Chang J, Costa OYA, Sun Y, Wang J, Tian L, Shi S, et al. Domesticated rice alters the rhizosphere microbiome, reducing nitrogen fixation and increasing nitrous oxide emissions. Nat Commun. 2025;16(1):2038. https://doi.org/10.1038/s41467-025-57213-x

69. Boyle JA, Frederickson ME, Stinchcombe JR. Genetic architecture of heritable leaf microbes. Microbiol Spectr. 2024;12(7):e00610-24. https://doi.org/10.1128/spectrum.00610-24

70. Pérez-Enciso M, Zingaretti LM, Ramayo-Caldas Y, de los Campos G. Opportunities and limits of combining microbiome and genome data for complex trait prediction. Genet Sel Evol. 2021;53(1):65. https://doi.org/10.1186/s12711-021-00658-7

71. Kim H, Lee KK, Jeon J, Harris WA, Lee YH. Domestication of *Oryza* species eco-evolutionarily shapes bacterial and fungal communities in rice seed. Microbiome. 2020;8(1):20. https://doi.org/10.1186/s40168-020-00805-0

72. Nguyen VH, Morantte RIZ, Lopena V, Verdeprado H, Murori R,

Ndayiragije A, et al. Multi-environment genomic selection in rice elite breeding lines. Rice. 2023;16(1):7. https://doi.org/10.1186/s12284-023-00623-6

73. Sanjenbam P, Buddidathi R, Venkatesan R, Shivaprasad PV, Agashe D. Phenotypic diversity of *Methylobacterium* associated with rice landraces in North-East India. PLoS One. 2020;15(2):e0228550. https://doi.org/10.1371/journal.pone.0228550

74. Muller E, Shiryan I, Borenstein E. Multi-omic integration of microbiome data for identifying disease-associated modules. Nat Commun. 2024;15(1):2621. https://doi.org/10.1038/s41467-024-46888-3

75. Sinha D, Maurya AK, Abdi G, Majeed M, Agarwal R, Mukherjee R, et al. Integrated genomic selection for accelerating breeding programs of climate-smart cereals. Genes (Basel). 2023;14(7):1484. https://doi.org/10.3390/genes14071484

76. Jyoti S Das, Singh G, Pradhan AK, Tarpley L, Septiningsih EM, Talukder SK. Rice breeding for low input agriculture. Front Plant Sci. 2024;15:1408356. https://doi.org/10.3389/fpls.2024.1408356

77. Zhang J, Liu YX, Zhang N, Hu B, Jin T, Xu H, et al. NRT1.1B is associated with root microbiota composition and nitrogen use in field-grown rice. Nat Biotechnol. 2019;37(6):676-84. https://doi.org/10.1038/s41587-019-0104-4

78. Blonde C, Caddeo A, Nasser W, Reverchon S, Peyraud R, Haichar F, el Z. New insights in metabolism modelling to decipher plant-microbe interactions. New Phytol. 2025;246(4):1485-93. https://doi.org/10.1111/nph.70063

79. Schmidt CM, Ghadermazi P, Chan SHJ. Predicting microbiome metabolism and interactions through integrating multidisciplinary principles. mSystems. 2021;6(5):e00768-21. https://doi.org/10.1128/msystems.00768-21

80. Edwards J, Johnson C, Santos-Medellín C, Lurie E, Podishetty NK, Bhatnagar S, et al. Structure, variation and assembly of the root-associated microbiomes of rice. Proc Natl Acad Sci U S A. 2015;112(8):E911-20. https://doi.org/10.1073/pnas.1414592112

81. Enespa, Chandra P. Tool and techniques study to plant microbiome current understanding and future needs: an overview. Commun Integr Biol. 2022;15(1):209-25. https://doi.org/10.1080/19420889.2022.2082736

82. Howe A, Stopnisek N, Dooley SK, Yang F, Grady KL, Shade A. Seasonal activities of the phyllosphere microbiome of perennial crops. Nat Commun. 2023;14(1):1039. https://doi.org/10.1038/s41467-023-36515-y

83. Meng W, Zhou Z, Tan M, Liu A, Liu S, Wang J, et al. Integrated analysis of metatranscriptome and amplicon sequencing to reveal distinctive rhizospheric microorganisms of salt-tolerant rice. Plants (Basel). 2024;14(1):36. https://doi.org/10.3390/plants14010036

84. Nwachukwu BC, Babalola OO. Metagenomics: a tool for exploring key microbiome with the potentials for improving sustainable agriculture. Front Sustain Food Syst. 2022;6:886987. https://doi.org/10.3389/fsufs.2022.886987

85. Quan G, Xia P, Lian S, Wu Y, Zhu G. Zinc uptake system ZnuACB is essential for maintaining pathogenic phenotype of F4ac(+) enterotoxigenic E. coli (ETEC) under a zinc restricted environment. Vet Res. 2020;51(1):127. https://doi.org/10.1186/s13567-020-00854-1

86. Thingujam D, Liu J, Majeed A, Mukhtar MS. Plant-microbiome dynamics through spatial metatranscriptomics and network biology. Trends Plant Sci. 2024;29(11):1176-80. https://doi.org/10.1016/j.tplants.2024.07.007

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

88. Soman R, Kavitha MH, Shaji H. Chapter 44 - Metagenomics: a genomic tool for monitoring microbial communities during bioremediation. In: Malik JA, editor. Microbes and microbial biotechnology for green remediation. Elsevier; 2022. p. 813-21 https://doi.org/10.1016/B978-0-323-90452-0.00006-2

89. Cai Z, Yu T, Tan W, Zhou Q, Liu L, Nian H, et al. GmAMT2.1/2.2-dependent ammonium nitrogen and metabolites shape rhizosphere microbiome assembly to mitigate cadmium toxicity. NPJ Biofilms Microbiomes. 2024;10(1):60. https://doi.org/10.1038/s41522-024-00532-6

90. Mueller UG, Linksvayer TA. Microbiome breeding: conceptual and practical issues. Trends Microbiol. 2022;30(10):997-1011. https://doi.org/10.1016/j.tim.2022.04.003

91. Wang M, Eyre AW, Thon MR, Oh Y, Dean RA. Dynamic changes in the microbiome of rice during shoot and root growth derived from seeds. Front Microbiol. 2020;11:559728. https://doi.org/10.3389/fmicb.2020.559728

92. Bruijning M, Ayroles JF, Henry LP, Koskella B, Meyer KM, Metcalf CJE. Relative abundance data can misrepresent heritability of the microbiome. Microbiome. 2023;11(1):222. https://doi.org/10.1186/s40168-023-01669-w

93. Gonçalves OS, Creevey CJ, Santana MF. Designing a synthetic microbial community through genome metabolic modeling to enhance plant-microbe interaction. Environ Microbiome. 2023;18(1):81. https://doi.org/10.1186/s40793-023-00536-3

94. Marco S, Loredana M, Riccardo V, Raffaella B, Walter C, Luca N. Microbe-assisted crop improvement: a sustainable weapon to restore holobiont functionality and resilience. Hortic Res. 2022;9:uhac160. https://doi.org/10.1093/hr/uhac160

95. Brachi B, Filiault D, Whitehurst H, Darme P, Le Gars P, Le Mentec M, et al. Plant genetic effects on microbial hubs impact host fitness in repeated field trials. Proc Natl Acad Sci U S A. 2022;119(30):e2201285119. https://doi.org/10.1073/pnas.2201285119

96. Oyserman BO, Flores SS, Griffioen T, Pan X, van der Wijk E, Pronk L, et al. Disentangling the genetic basis of rhizosphere microbiome assembly in tomato. Nat Commun. 2022;13(1):3228. https://doi.org/10.1038/s41467-022-30849-9

97. He X, Wang D, Jiang Y, Li M, Delgado-Baquerizo M, McLaughlin C, et al. Heritable microbiome variation is correlated with source environment in locally adapted maize varieties. Nat Plants. 2024;10(4):598-617. https://doi.org/10.1038/s41477-024-01654-7

98. He X, Zhang Q, Li B, Jin Y, Jiang L, Wu R. Network mapping of root-microbe interactions in *Arabidopsis thaliana*. NPJ Biofilms Microbiomes. 2021;7(1):72. https://doi.org/10.1038/s41522-021-00241-4

99. Chen L, Bao H, Yang J, Huo Y, Zhang J, Fang R, et al. Dynamics of rice seed-borne bacteria from acquisition to seedling colonization. Microbiome. 2024;12(1):253. https://doi.org/10.1186/s40168-024-01978-8

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.