*Review Article*

**Microbial Communities in Rice: Their Contribution to Nutrient Dynamics and Yield Enhancement**

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ABSTRACT

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| Plants are in a dynamic web of biotic and abiotic associations, commonly called the phytobiome. Of the biotic components, the plant microbiome is at the core of managing plant health, growth, and productivity. Understanding the structure and function of microbial populations that live in association with plants is key to understanding plant-microbe interactions and their influence on crop performance. Rice (Oryza sativa L.), a food source for over half the world's population, is faced with mounting production issues with limited arable land, soil erosion, and unsustainable agriculture. These have resulted in amplified application of chemical fertilizers, which is environmentally costly and has generated interest in microbial alternatives as sustainable inputs. Despite significant research on microbial inoculants, their effective utilization is sporadic. This review considers the diversity and functional importance of the rice microbiome, in terms of its function in agricultural quality and yield. It also considers the prospect of harnessing microbial communities as sustainable biofertilizers to enhance rice productivity. A comprehensive understanding of the rice microbiome in a range of environmental conditions may make it feasible to design optimized microbial interventions tailored to a specific agricultural environment. |

*Keywords: microbiome, microbes, rice, yield, nutrients, rhizosphere, sustainable agriculture*

1. INTRODUCTION

Plants encounter a huge range of biotic and abiotic factors throughout their lives, which are together referred to as the phytobiome. It is a complex system which includes plants and their surrounding environment, with dynamic interaction between both abiotic and biotic factors (Leach *et al.* 2017). These interactions influence both natural ecosystems and agroecosystems. Among the biotic factors, a crucial role is played by the microbial communities associated with plants, known as the microbiota or plant microbiome (Müller and Ruppel,2014). Understanding the factors affecting community assembly and the plant-microbe interactions can improve our comprehension of plants as meta-organisms and reveal how they benefit from their microbial partners (Hardoim *et al.*, 2015; Hacquard, 2016).

Rice (*Oryza sativa* L., 2n = 2x = 24) as a staple food for more than half of the world’s population, is the globe's second most widely consumed cereal, providing 30% of the calories consumed in Asian countries. According to the Food and Agriculture Organization (FAO), currently 38.7% of the world’s land area is designated as agricultural land, among which 28.43% is arable land (Gouda *et al*., 2018). However, the arable land availability is declining continuously pertaining to the rapid urbanization and industrialization which have intensified environmental degradation (Goswami and Deka, 2020; Gouda *et al*., 2018). Since the expansion of arable land is not an option, there has been a widespread use of chemical fertilizers as plant nutrients to meet the increasing demand for rice production, which poses a significant environmental risk to arable land (de Souza *et al*., 2015). In recent years, rice yields have seen a stagnating and declining trend, mainly due to over-exploitation and mismanagement of soil, raising concerns about the long-term sustainability of rice cropping systems globally (Bhatt *et al*., 2016). Interestingly, microorganisms have demonstrated potential both as biopesticides and biofertilizers, which has led to the increasing interest in integrating these biological agents as chemical product alternatives in agriculture (Mendes *et al.,* 2013; Mitter *et al.* 2016). The research into microbial inoculants dates back to the 80s (Glick, 2012), however the field applications have seen limited success. A deeper understanding of the plant microbiome in relation to the performance of crops in diverse environmental conditions could help identify more effective microbial inoculation approaches and candidates for each specific environment (Mitter *et al.* 2016). This review mainly focuses on the general diversity of rice microbiome, and its interaction with the agricultural quality and production.

**2. RICE MICROBIOME**

Microbiomes are found throughout and around rice plants. The rice microbiome can be compartmentalised according to where microbial communities reside: rhizosphere, phyllosphere, endosphere, bulk soil and seeds. Among these, the most extensively studied ones are the bulk soil and the root system (including the rhizosphere and root endosphere).

**2.1 Bulk Soil**

Also known as unplanted soil, bulk soil is the most researched aspect of paddy fields. It has a key role in organic matter and mineral accumulation, nutrient cycling and capturing air and water (Karlen *et al.* 1997; Chaudhary *et al.* 2013). For these functions, the soil microbial communities are much essential, as they promote organic matter decomposition and enhance nutrient availability. Generally, the soil bacterial community is dominated by *Proteobacteria*, *Actinobacteria* and *Acidobacteria* (Hussain *et al*. 2012; Jiang *et al*. 2016) while *Ascomycota, Basidiomycota* and *Glomeromycota* are known to dominate the fungal community in rice fields (Jiang *et al*. 2016; Yuan *et al*. 2018).

**2.2 Rhizosphere**

The soil that closely surrounds plant roots, known as the rhizosphere, is a dynamic zone where roots exert profound influence by secreting inorganic and organic compounds, known as root exudates. These exudates which nurtures the intimate connection between roots and soil, facilitates root growth, and ensures the plant's survival are quite vital (Walker *et al.* 2003). They enable plants to adapt well to their soil environment and supply essential nutrients which helps in attracting and establishing beneficial soil microbes (Bacilio-Jiménez *et al.* 2003). While doing so, root exudates elevate the biological richness of the rhizosphere, offering plants a nutrient reservoir, plant hormones, pathogen resistance, and improved resilience against environmental stresses like drought (Bacilio-Jiménez *et al.* 2003; Bhuvaneswari and Subba-Rao 1957; el Zahar Haichar *et al.* 2008; Lu *et al.* 2004; Saleem *et al.* 2018). The rice rhizosphere, like that of other plants, is the most biodiverse environment among the compartments. This rich microbial diversity of the rhizosphere is a clear indication that in comparison to other compartments, the rhizosphere has greater prevalence of the beneficial microbes, which protect rice plants from pathogens or promote their growth. Indeed, through both *in vitro* and *in vivo* analyses, bacterial isolates belonging to *Pseudomonas* spp. have been identified and characterized (Spence *et al.* 2014). Moreover, it has been discovered that the systemic resistance response in rice can be triggered by rhizospheric bacteria, mediated by jasmonic acid and ethylene.

**2.3 Phyllosphere**

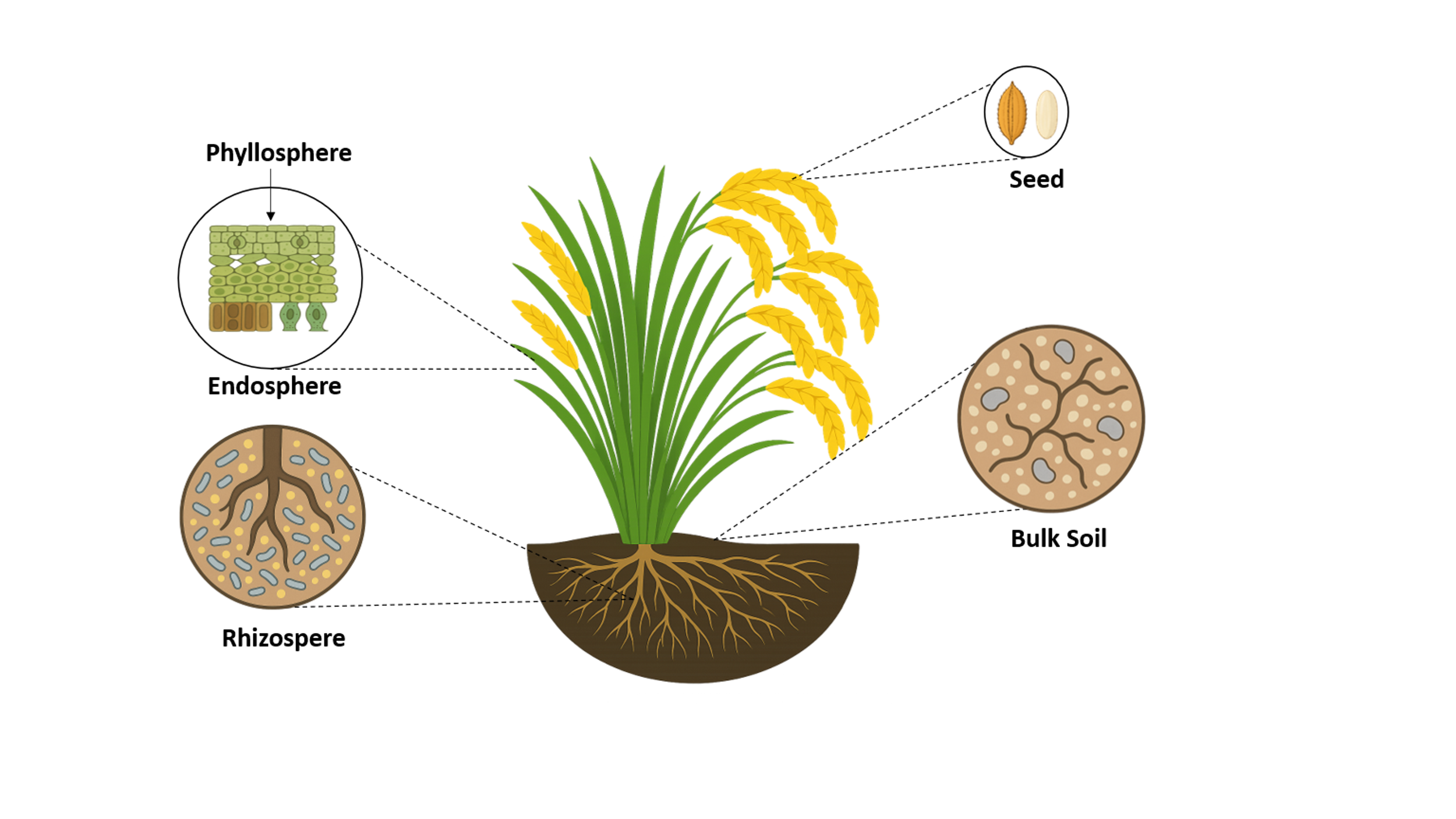
The phyllosphere consisting of the above ground parts of plants, is a home to a vibrant community of bacteria, fungi, protists and archaea, despite the challenges posed by ultraviolet radiation, limited nutrients, rapid temperature fluctuations and scarcity of water (Müller and Ruppel 2014). Most of these microbes are commensal and quite difficult to culture, leading to researchers exploring their communities using advanced, culture-independent techniques like 16S or 18S rRNA gene sequencing (de Souza *et al.* 2016). Studies of phyllosphere microbiomes have dug into the factors shaping these communities, the origins of their inhabitants, their genetic and functional characteristics, and the crucial role they play in stress adaptation of plants. (Rastogi *et al.* 2013).

**2.4 Endosphere**

The inner tissues of plant parts like leaves, stems, roots, fruits, and seeds are called endosphere, where a diverse array of microorganisms, known as endophytes, reside. Endophytes can be put into different categories based on their effects on plants. The neutral category exerts little impact, while the beneficial ones enhance plant growth or provides protection against pathogens and herbivores. A third group referred to as opportunistic or latent pathogens, may cause harm under certain conditions (Hardoim *et al.* 2015). Among these categories, beneficial endophytes are increasingly recognized as valuable resources for biocontrol agent and biofertilizer development, which presents promising opportunities to boost crop productivity. Numerous studies have explored these endophytes using next-generation sequencing (NGS) technologies, along with efforts to collect and characterize endophytic isolates through culture-dependent methods across various plants (Mano and Morisaki 2008; Sun *et al.* 2008; Yuan *et al.* 2010; Gottel *et al.* 2011; Sessitsch *et al.* 2012; Bertani *et al*. 2016; de Souza *et al.* 2016; Sengupta *et al*. 2017). However, technical challenges are faced while researching on endospheric microbiomes, particularly due to the overshadowing of the relatively small contribution from endophytes in comparison to the overwhelming presence of host plant genomic DNA. A significant issue is the co-amplification of plastid and mitochondrial DNA during the generation of bacterial amplicons. The high host-to-endophyte DNA ratio results in low sequencing depth and compromised quality in the raw sequence data of the endophyte.

**2.5 Seed**

Seeds are the major reservoirs of nutrients necessary for germination and early plant development, before the plants can become autotrophic through photosynthesis. Moreover, the seeds support complex microbial communities, including bacteria, fungi and viruses, which can improve the viability of plants by ensuring maximum quality of seeds and shielding newly germinated seedlings from pathogen attacks (Shade *et al.* 2017; Nelson 2018). Despite their importance, seed microbiomes are poorly characterized. In rice, culture-dependent methods have identified bacteria like *Bacillus firmus*, *B. fusiformis*, *B. pumilus*, *Caulobacter crescentus*, *Kocuria palustris*, *Micrococcus luteus*, *Methylobacterium fujisawaense*, *Methylobacterium radiotolerans* and *Pantoea ananatis* from the seed microbiome (Kaga *et al*. 2009). Besides, fungal cultures including saprobes and potential plant pathogens like *Alternaria alternata*, *Cladosporium tenuissimum*, *Epicoccum purpurascens*, *Fusarium equiseti*, *F. oxysporum*, and *Phoma sorghina* have been obtained from surface-sterilized seeds (Fisher and Petrini 1992).



**Fig. 1. Illustration of components of rice microbiome *viz.* seed, phyllosphere, endosphere, bulk soil and rhizosphere.**

**3. EFFECT OF RICE MICROBIOME ON NUTRIENT AVAILABILITY**

The rice microbiome is pivotal in enhancing the delivery of nutrients at the soil-plant interface by enabling a variety of core biogeochemical processes. Microorganisms such as the rhizosphere microbes are essential in the cycling and bioavailability of major nutrients, including both macronutrients and micronutrients. Microorganisms such as *Azospirillum* and *Rhizobium* enable the reduction of atmospheric nitrogen to ammonia through nitrogen fixation, thereby providing a sustainable source of the crucial macronutrient. Phosphate-solubilizing microbes such as *Pseudomonas* and *Bacillus* species release phosphorus in soluble form through enzymatic activity and organic acid production, thereby alleviating the phosphorus shortages encountered in agricultural soils. Additionally, potassium-solubilizing bacteria release potassium from mineral deposits, thereby enhancing plant uptake. Siderophore-producing microorganisms enhance the availability of micronutrients, including iron, by chelating ferric ions, thereby enhancing their availability to rice roots (Timofeeva *et al.* 2023). The mode of interaction among these microbes not only enhances the efficiency of nutrient uptake but also governs the nutritional quality of rice grains (Table 1). The utilization of the rice microbiome offers a promising strategy in sustainable agriculture as it lowers chemical fertilizer application, enhances the health of soils and enables one to construct resilience against environmental stressors.

Iron (Fe) is a critical micronutrient for all soil microbes and its bioavailability is often limited (Tariq *et al*., 2007). Siderophores, low molecular weight compounds secreted by microorganisms, chelate Fe³⁺, enabling its transport back to microbial cells and promoting microbial growth (Meyer, 2000). Certain plant growth promoting bacteria (PGPB) produce siderophores that are absorbed by plant roots, serving as an iron source for plant cells (Sharma and Johri, 2003). Production of siderophores has been described in a variety of microorganisms, including *Bacillus*, *Pseudomonas,* *Azotobacter*, *Arthrobacter*, *Burkholderia*, *Enterobacter*, *Rhodospirillum*, *Serratia*, *Azospirillum* and *Rhizobium*. In the rhizosphere, PGPB siderophores play two key roles: (a) promotion of plant growth by enhancing iron availability for nutrient uptake and (b) suppression of soil-borne pathogens by creating iron-limited conditions and therefore suppressing pathogen growth (Tariq *et al*., 2007; Saha *et al*., 2016; Delaporte-Quintana *et al*., 2020). A study on *Oryza sativa* (rice) by Loaces *et al*. (2011) indicated that rice roots were colonized with siderophore-producing bacteria (SPB) compared to that of the surrounding soil. To investigate the beneficial activities of microbial siderophores towards rice, a pot culture experiment was conducted using *Streptomyces* sp. GMKU 3100, a siderophore-producing bacterium isolated from Thai Jasmine rice roots. The results indicated that plants inoculated with the wild-type strain exhibited the most remarkable improvements in plant growth, root and shoot biomass compared to controls and plants inoculated with the mutant strain (Rungin *et al*., 2012). *Geobacter* and *Shewanella* are the most commonly described Fe (III)-reducing bacteria (FeRB) (Weber *et al*., 2006) and are commonly isolated from the rice rhizosphere (Wang *et al*., 2009; Zecchin *et al*., 2017). Fe-reducing bacteria (FeRB) constitute approximately 12% of the overall bacterial population in the rhizosphere and less than 1% in bulk soil (Weiss *et al*., 2004). Surprisingly, higher densities of FeRB have been reported in the rhizosphere compared to bulk soil (Chen *et al*., 2008), resulting in Fe reduction rates that are almost twice those occurring in non-rhizosphere soils (Weiss *et al*., 2004). This heightened activity is attributed to the higher concentrations of Fe (III) that occur on root surfaces (Tian *et al*., 2015).

Rice is also very prone to zinc (Zn) deficiency, a situation that causes malnutrition in rice-dependent populations, especially in Asia (Krithika and Balachandar, 2016). Inoculation with plant growth-promoting bacteria (PGPB) was found to reduce Zn deficiency symptoms, enhancing total biomass by 23%, grain yield by 65%, and soil Zn content (Tariq *et al*., 2007). Zn-solubilizing bacteria like *Bacillus* spp. espicially *Bacillus cereus* effectively enhanced Zn translocation to grains, enhancing yields of rice varieties Basmati-385 and Super Basmati by 22–49% and 18–47%, respectively (Shakeel *et al*., 2015). Furthermore, *Pseudomonas* strains were found to enhance Zn content in roots, shoots and grains by 1.5–2-fold compared to controls, leading to enhanced rice growth and yield (Sharma *et al*., 2015). Moreover, *Burkholderia* and *Acinetobacter* strains enhanced overall Zn uptake per pot by 52.5% and grain methionine concentration by 38.8%, further proving their potential to enhance rice nutrition and productivity (Vaid *et al*., 2014). Phosphate-solubilizing bacteria (PSB) constitute 1–50% of the total microbial population in soil (Gyaneshwar *et al*., 2002). Various bacterial genera, including *Bacillus*, *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Delftia*, *Gordonia*, and *Phyllobacterium*, exhibit phosphate-solubilizing activity (Chen *et al*., 2006). In aerobic rice systems, inoculation with the *Bacillus* spp*.* PSB16 strain resulted in significant phosphate solubilization (24.08 mg kg⁻¹) and increased plant phosphorus (P) uptake (5.31 mg plant⁻¹) at a P application rate of 60 kg ha⁻¹. Similarly, inoculation with two *Bacillus* strains enhanced soluble P levels, plant P uptake, and organic acid concentrations in rice roots after 60 days (Panhwar *et al*., 2011).

Tang *et al*. (2021) reported that inoculation of rice plants with the endophytic fungus *Phomopsis liquidambaris* caused significant increases in plant growth, yield, grain quality and mineral nutrition. Transcriptomic analysis revealed upregulation of genes involved in nitrogen (N) transport (e.g., *Os*AMT1;4 and *Os*NRT1;1) and phosphorus (P) transport (e.g., *Os*PT1 and *Os*Pht1;2) at the seedling stage after inoculation with *P. liquidambaris*. Similar upregulation was found for the transporter genes at the heading stage, including genes that are involved in the uptake of phosphorus, zinc and iron in rice roots (*Os*PT1, *Os*Pht1;2, *Os*ZIP3, *Os*ZIP4, *Os*IRT1, and *Os*IRT2). In addition, genes involved in the transport of N, P, Zn and Fe (*Os*AMT1;4, *Os*Pht1, *Os*ZIP4 and *Os*IRT1) also showed increased expression levels. In the ripening stage, significant changes in the expression of genes involved in Zn and Fe transport (*Os*ZIP3 and *Os*IRT2) and the transport of P, Zn, and Fe (*Os*Pht1;2, *Os*ZIP3, *Os*ZIP4 and *Os*IRT1) were observed.

**Table 1: Reported experiments on the influenced of microbes on nutrient content**

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| **Microbes** | **Effect on nutrient availability** | **Location** | **Reference** |
| *Bacillus, Rhodococcus, Arthrobacter, Serratia, Chryseobacterium, Delftia, Gordonia and Phyllobacterium* | Increase in phosphate solubilization and intake | Rhizosphere | Panhwar *et al.*, 2011 |
| *Bacillus cereus, Pseudomonas spp.* | Increase in Zn content in rice grains | Rhizosphere | Shakeel *et al.*, 2015 |
| *Phomopsis liquidambaris* | Increase in N and P during seedling stage and increase in N, P, Zn and Fe during heading stage | Endosphere | Tang *et al.* 2021 |

**4. EFFECT OF RICE MICROBIOME ON YIELD**

Grain yield is defined by management practices that are indicative of the productivity capability of the crop environment. Its development occurs in three stages: vegetative (emergence through panicle initiation), reproductive (panicle initiation through flowering), and spikelet-filling (flowering through maturity). These stages as a whole define the potential yield of rice, and important development processes take place at each stage (Fageria, 2007).

Root microbiota play an important role in increasing rice yield (Table 2). Plant age, development phase, root architecture and exudation behaviour regulate root-associated microbial populations, which in turn, regulate bacterial diversity trajectory (Edwards *et al*., 2018). Microbial composition and functional gene expression changes during the growth phase are key to rice yield increase (Wang *et al*., 2019).

**Table 2: Reported studies demonstrating microbial communities enhancing the physiological status and yield of rice.**

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| **Microbes** | **Effect on yield and yield attributing traits** | **Location** | **Reference** |
| *Azospirillum sp.* | Promoted early tillering and the better reproductive performance of rice plants. It was found to significantly increase the grain-filling rate and the grain weight per plant at harvest time | Rhizosphere | Watanabe *et al.* 1984 |
| *Beijerinckia indica* | Enhanced number of tillers and plant height | Phyllosphere | Pati, 1992 |
| *R. leguminosarum E11; Rhizobium sp. IRBG74; and Bradyrhizobium sp. IRBG271* | Enhanced shoot biomass and NPK uptake | Rhizosphere | Biswas *et al.,* 2000 |
| *Pseudomonas fluorescens* | Inoculation with mixture of PGPR (plant growth promoting rhizobacteria) strains to the rice plant significantly promoted grain yield. The average yield enhancement was 17.7%, for single strains and 25.9% in case of mixture. | Rhizosphere | Nandakumar *et al.*, 2001 |
| *Anabaena variabilis, Tolypothrix tenuis, Nostoc muscorum, and Aulosira fertilissima* | Enhanced grain yield | Rhizosphere | Dhar *et al.,* 2007 |
| *Pseudacidovorax* sp.*, Rhizobium* sp.*, Azospirillum* sp., *Pseudomonas* sp*., Candida* sp.*, Bacillus amyloliquefaciens, Bacillus subtilis* | Increasing grain and straw yields, total N uptake. | Rhizosphere | Cong *et al.*, 2009 |
| Seven rice endophyte strains of *Rhizobium leguminosarum bv. trifolii* | Inoculation with single strains or multi-strain consortia significantly promoted grain yield. Grain yield was increased up to 47% in field experiment. | Rhizosphere | Yanni and Dazzo, 2010 |
| *Herba*sp*irillum* sp*., Burkholderia* sp. | Enhancement of NPK uptake, dry shoot and grain production, though chemical fertilizer was diminished in half. | Rhizosphere | Souza *et al.*, 2013 |
| *Bacillus spo.* | improved yield as well as yield related parameters such as plant height, tillering and panicle length. | Rhizosphere | Shakeel *et al.*, 2015, Rais *et al.*, 2016 |
| *Lysinibacillus xylantilyticus, Alcaligenes faecalis, Bradyrhizobium japonicum, Rhizobium etli, Bacillus subtilis* | The significant effects of beneficial bacterial inoculations appeared due to plant growth promotion activities. Isolated indigenous PGPR and rhizobial strains have the potential to increase growth and yield of rice by minimizing Nitrogen fertilizer use. | Rhizosphere | Ali-Tan *et al*., 2017 |
| *Burkholderia* sp., *Pseudomonas aeruginosa* | Application of two most efficient phosphate solubilizing bacteria by root dipping (colonization) during seedling stage and administrating at the flowering stage significantly increased the growth and grain yield of rice variety BRRI dhan-29 with reduction of major fertilizers utilization. | Rhizosphere | Khan *et al.*, 2017 |
| *T. asperellum* | Enhances rice germination, seedling and vegetative growth, plant vigour, grain yield, photosynthetic rate, stomatal conductance, and water-use efficiency of rice plants | Rhizosphere | Doni *et al.,* 2019 |
| *Trichoderma sp.* | Significant increase in plant growth and grain yield | Endosphere | Khadka *et al.*, 2019 |

**5. CONCLUSION**

The rice microbiome is a vast resource for revolutionizing sustainable agriculture by restraining its dependence on chemical inputs and enhancing crop productivity. With our expanding knowledge of plant-microbe interactions, opportunities arise to leverage microbial communities to enhance nutrient uptake, stress tolerance, and disease resistance in rice. Although controlled experiments have been encouraging, variable field performance of microbial inoculants highlight the imperative need for more targeted research to bridge the gap between laboratory and field-scale applications. Future research should be aimed at characterizing and modifying microbial consortia to local environmental and cropping conditions using state-of-the-art technologies such as metagenomics, transcriptomics, and metabolomics. Designing predictive models to unravel microbial assembly and function in complex ecosystems will enable the development of precision agriculture concepts. Furthermore, the convergence of microbiome-focused approaches with other sustainable practices such as conservation agriculture and integrated pest management can revolutionize rice cultivation into an improved and environmentally sustainable system. By focusing research on the rice microbiome and its applications, we can build the foundations for innovation to enable food production with environmental integrity for the next generation.

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