



Optimizing iron Manganese, and Zinc Fertilization in Rice (*Oryza sativa* L.) through *Bacillus*, *Pseudomonas*, and *Aspirillum* Bacteria*

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Abstract: Rice (*Oryza sativa*) is a cereal crop crucial for global food security. However, the limited availability of micronutrients such as Iron (Fe), Manganese (Mn), and Zinc (Zn) in calcareous soils can lead to metabolic disturbances in the plant, resulting in various anomalies. These disturbances can reduce yields and, in severe cases, lead to plant death. Plant growth-promoting microorganisms found in the soil rhizosphere can solubilize these micronutrients. These microorganisms have also been isolated from soils and utilized as biostimulants and biofertilizers, facilitating their use in optimizing rice cultivation. The objective of this study was to conduct a literature review on *Bacillus*, *Pseudomonas* and *Azospirillum* and their ability to solubilize Fe, Mn, and Zn rice cultivation. The study describes the nature, assimilation, and importance of these three micronutrients in soil and in rice cultivation, as well as the optimization of the microorganisms as ingredients that promote crop growth and productivity. Furthermore, it discusses their mechanisms, such as the secretion of the siderophores deoxymugenic acid (DMA) and mugenic acid (MA), the production of organic acids like indole-3-acetic acid (IAA) and abscisic acid, the production of phytohormones (e.g., cytokinins), and a network of metalloproteins that facilitate soil acidification. These mechanisms enable the solubilization of Fe, Mn, and Zn in the soil associated with the crop, making them available for absorption by the root system in the form of chelates. To sum up, the addition of *Bacillus*, *Pseudomonas* and *Azospirillum* facilitates the absorption of micronutrients in the crop and mitigates the negative effects caused by the constant application of chemical fertilizers, which can accumulate in plant tissue, soil, and water.

Keywords: Micronutrients; Iron; Manganese; Zinc; Bacteria; Biofertilizer; Biostimulant

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Optimización de la fertilización con hierro, manganeso y zinc en arroz (Oryza sativa L.) a través de bacterias Bacillus, Pseudomonas y Azospirillum

Resumen: El arroz (*Oryza sativa*) es un cultivo de cereal crucial para la seguridad alimentaria mundial. Sin embargo, la disponibilidad limitada de micronutrientes como el hierro (Fe), manganeso (Mn) y zinc (Zn) en suelos calcáreos puede provocar trastornos metabólicos en la planta, lo que resulta en diversas anomalías. Estos trastornos pueden reducir los rendimientos y, en casos graves, llevar a la muerte de la planta. Los microorganismos promotores del crecimiento vegetal presentes en la rizosfera del suelo pueden solubilizar estos micronutrientes. Estos microorganismos también se han aislado de suelos y se han utilizado como biestimulantes y biofertilizantes, facilitando su uso en la optimización del cultivo de arroz. El objetivo de este estudio fue realizar una revisión bibliográfica sobre *Bacillus*, *Pseudomonas* y *Azospirillum* y su capacidad para solubilizar Fe, Mn y Zn en el cultivo de arroz. El estudio describe la naturaleza, asimilación e importancia de estos tres micronutrientes en el suelo y en el cultivo de arroz, así como la optimización de los microorganismos como ingredientes que promueven el crecimiento y la productividad de los cultivos. Además, se discuten sus mecanismos, como la secreción de sideróforos ácido deoximugénico (DMA) y ácido mugénico (MA), la producción de ácidos orgánicos como el ácido indol-3-acético (IAA) y el ácido abscísico, la producción de fitohormonas (por ejemplo, citocininas) y una red de metaloproteínas que facilitan la acidificación del suelo. Estos mecanismos permiten la solubilización de Fe, Mn y Zn en el suelo asociado al cultivo, haciéndolos disponibles para su absorción por el sistema de raíces en forma de quelatos. En resumen, la adición de *Bacillus*, *Pseudomonas* y *Azospirillum* facilita la absorción de micronutrientes en el cultivo y mitiga los efectos negativos causados por la aplicación constante de fertilizantes químicos, que pueden acumularse en los tejidos de las plantas, el suelo y el agua.

Palabras clave: micronutrientes; hierro; manganeso; zinc; bacterias; biofertilizante; Biestimulante

Otimização da fertilização com ferro, manganês e zinco em arroz (Oryza sativa L.) através de bactérias Bacillus, Pseudomonas e Azospirillum

Resumo: O arroz (*Oryza sativa*) é um cultivo de cereal crucial para a segurança alimentar mundial. No entanto, a disponibilidade limitada de micronutrientes como ferro (Fe), manganês (Mn) e zinco (Zn) em solos calcários pode provocar distúrbios metabólicos na planta, resultando em diversas anomalias. Esses distúrbios podem reduzir os rendimentos e, em casos graves, levar à morte da planta. Os microrganismos promotores do crescimento vegetal presentes na rizosfera do solo podem solubilizar esses micronutrientes. Esses microrganismos também têm sido isolados de solos e utilizados como bioestimulantes e biofertilizantes, facilitando seu uso na otimização do cultivo de arroz. O objetivo deste estudo foi realizar uma revisão bibliográfica sobre *Bacillus*, *Pseudomonas* e *Azospirillum* e sua capacidade de solubilizar Fe, Mn e Zn no cultivo de arroz. O estudo descreve a natureza, assimilação e importância desses três micronutrientes no solo e no cultivo de arroz, bem como a otimização dos microrganismos como ingredientes que promovem o crescimento e a produtividade dos cultivos. Além disso, discutem-se seus mecanismos, como a secreção de sideróforos ácido deoximugínico (DMA) e ácido mugínico (MA), a produção de ácidos orgânicos como o ácido indol-3-acético (IAA) e o ácido abscísico, a produção de fitohormonas (por exemplo, citocininas) e uma rede de metaloproteínas que facilitam a acidificação do solo. Esses mecanismos permitem a solubilização de Fe, Mn e Zn no solo associado ao cultivo, tornando-os disponíveis para a absorção pelo sistema radicular na forma de quelatos. Em resumo, a adição de *Bacillus*, *Pseudomonas* e *Azospirillum* facilita a absorção de micronutrientes no cultivo e mitiga os efeitos negativos causados pela aplicação constante de fertilizantes químicos, que podem se acumular nos tecidos das plantas, no solo e na água.

Palavras-chave: micronutrientes; ferro; manganês; zinco; bactérias; biofertilizante; bioestimulante

Introduction

Rice (*Oryza sativa* L.) is a Poaceae plant that serves as a staple food for 3.5 billion people globally, with an average per capita consumption of 54.1 kg per year. In 2020, the global harvested area of rice reached 164,192,164 hectares, yielding 46,089 kg per hectare and totaling 756,743,722 tons in production. Asia accounted for 90% of the world's rice production, followed by Africa and Latin America (Nadeem and Farooq, 2019; FAOSTAT, 2020; Shrestha et al., 2020; Keerthana and Lavanya, 2022). Rice cultivation is historically rooted in tropical and subtropical regions with humid and temperate climates, typically found between 49° and 50° latitude North and 35° latitude South, and at elevations ranging from sea level to 2,500 meters. These regions typically experience temperatures between 16°C and 32°C and receive approximately 1,020 mm of annual precipitation (Maqueria et al., 2016; Azziz et al., 2017; Infoagro, n.d.).

Rain-fed and irrigated rice cultivation predominantly occurs on lands with slopes lower than 20% and soil pH ranging from 5.5 to 6.6, consisting of loamy, sandy clay, or clay loam soils. Conversely, upland rice is grown in soils with a pH levels lower than 5 or higher than 9 (Chauhan et al., 2017; Quintero, 2018; Infoagro, 2020). The rice crop has a life cycle of approximately 150 days, during which it extracts around 110 kg of N, 34 kg of P₂O₅, 156 kg of K₂O, 23 kg of MgO, 20 kg of CaO, 5 kg of S, 2 kg of Fe, 2 kg of Mn, 200 g of Zn, 150 g of Cu, 150 g of B, 250 kg of Si, and 25 kg of Cl per hectare from the soil (Chauhan et al., 2017; Quintero, 2018). These macronutrients are crucial for growth, while micronutrients such as iron (Fe), manganese (Mn), and zinc (Zn) play essential roles in protein synthesis, enzymatic activation processes, and biochemical activities contributing to high grain yields (Zayed et al., 2011; Nadeem and Farooq, 2019; Shrestha et al., 2020).

Biofertilizers containing microorganisms such as *Bacillus*, *Pseudomonas*, and *Azospirillum* have demonstrated benefits in promoting robust growth, high yields, and grain quality in rice cultivation. Their application is increasingly important for preserving ecosystem functional biodiversity

(Saravanan et al., 2011a; Gontia-Mishra et al., 2017; Gusain and Sharma, 2019).

These microorganisms possess active mechanisms for solubilizing both macro and micronutrients, enhancing the absorption of less mobile nutrients by plant roots and meeting fertilizer requirements for optimal growth and development (Saravanan et al., 2011a; Alori and Babalola, 2018; Dal Cortivo et al., 2018; Dal Cortivo et al., 2020). Considering the aforementioned, a literature review was conducted to assess whether the utilization of microorganisms from the genera *Bacillus*, *Pseudomonas*, and *Azospirillum* contributes to the solubilization of the micronutrients iron (Fe), manganese (Mn) and zinc (Zn) in rice cultivation.

Methodology

The methodology involved conducting a literature review on the three microorganisms (*Bacillus*, *Pseudomonas*, and *Azospirillum*), and their relation to the fertilization of the micronutrients Fe, Mn, and Zn in rice cultivation. The review proceeded in the following sequence:

1. Nature and importance of the three micronutrients for cultivation, focussing their assimilation. The search engines used were Sciencedirect (44%), Google Scholar (19%), SpringerLink (16%), Researchgate.net (9%), PubMed (6%), Scopus (4%), Books (1%).
2. Examination of the principal microorganisms responsible for solubilizing the three micronutrients. Seventeen articles were reviewed, gathered from Google Scholar (19%), Scopus (19%), SpringerLink (19%), Researchgate.net (19%), Google (12%). Frontiers (6); Sciencedirect (6%).
3. Exploration of the characteristics and application of key biofertilizers containing solubilizing microorganisms for the three micronutrients. This step involved reviewing six literatures sources, primarily from SpringerLink (50%), Google Scholar (25%), and Sciencedirect (25%).
4. Analysis of the mechanisms underlying the solubilization of the three micronutrients by *bacillus*, *pseudomonas*, and *azospirillum* microorganisms. A total of 29 reviews were

conducted, with sources including Scopus (35%), SpringerLink (17%), Google Scholar (17%), Books (10%), Sciencedirect (7%), Researchgate.net (7%), Frontiers (4%), PubMed (3%).

The reviews encompassed articles, books, conference proceedings, and technical documents, with 93% of the content in English and 7% in Spanish. Journals included in the review were indexed, with 73% of the reviews focusing on the past ten years.

Geographical distribution of the reviewed information included: 51% from Asia (India, Japan, China, Pakistan, Nepal), 17% from Europe (Germany, Italy, Spain, Switzerland, Brussels, France, Greece, the United States, Austria, the Czech Republic), 21% from the Americas (USA, Brazil, Mexico, Argentina, Chile, Colombia, Uruguay), 12% from Africa, and 4% from Oceania (Australia).

Commercially available biofertilizer information was sourced from the Spanish Ministry of Agriculture, Fisheries, and Food of the Government (MAPA) and the Colombian Agricultural Institute (ICA).

Results

The Nature, Assimilation, and Importance of Micronutrients Fe, Mn, and Zn in Rice Cultivation

Nature

In soil, iron (Fe) exists in various forms, including hematite (Fe_2O_3), magnetite (Fe_3O_4), ferrihydrite $\text{Fe}(\text{OH})_3$, goethite ($\alpha\text{-FeOOH}$), and amorphous iron (Lindsay, 1979; Navarro and Navarro, 2013; Wu et al., 2021). Fe_2O_3 remains stable at high pH levels and persists under oxidizing conditions, contributing to the investigation of microbial reduction of Fe (III) (Li et al., 2018). Additionally, lepidocrocite and goethite (FeOOH) have been detected in significant quantities in soils, of 16 g kg^{-1} , along with amorphous iron minerals at 98.5 mg kg^{-1} (Chen, Dixon and Turner, 1980; Liu et al., 2010; He et al., 2021).

Manganese (Mn) minerals in soil include pyrolusite (MnO_2), hausmannite (Mn_3O_4), birnesite $\delta\text{-MnO}_2$, manganite ($\text{Mn}_2\text{O}_3 \cdot \text{H}_2\text{O}$), and rhodochrosite (MnCO_3) (Navarro and Navarro, 2013; Suda and Makino, 2015; Sinha and Purcell, 2019). For instance, the addition of hausmannite to potted rice (at $1200 \text{ mg Mn kg}^{-1}$ of soil) slows down the decrease in pH, demonstrating its influence on soil dynamics.

Zinc (Zn) in soil is present as minerals such as zincite (ZnO), sphalerite (ZnS), smithsonite (ZnCO_3), zinc sulfate (ZnSO_4), and franklinite ($\text{Zn-Fe}_2\text{O}_4$) (Saravanan, Kumar and Sa, 2011b; Kumar, Dewangan, Lawate, Bahadur, and Prajapati, 2019). These forms can exhibit various solubilities and availabilities, depending on factors such as soil pH, exchangeable, adsorbed, chelated, or in the form of secondary clay minerals or primary minerals (Alloway, 2008; Navarro and Navarro, 2013; Noulas, Tziouvakas and Karyotis, 2018). The solubility of Zn oxides and carbonates in alkaline soils can be limited. These forms can exhibit various solubilities and availabilities, depending on factors such as soil pH, are not rock composition, organic matter content, the texture, temperature, flooding, and the pH (Pradhan et al., 2021).

Assimilation

The solubility of Fe in soil is influenced by pH, redox conditions, and soil composition (Lindsay and Norvell, 1978; Navarro and Navarro, 2013; Lucena and Hernández-Apaolaza 2017; Sheng et al. 2021). In calcareous soils, approximately 0.5% of the total Fe is predominantly regulated by Fe (III) oxides, with soluble oxides such as ferrihydrite in highly oxidized soils and siderite in reduced soils playing significant roles (Lucena and Hernández-Apaolaza, 2017; Thorat, 2021; Rasheed, 2023). Rice cultivation occurs in two ecosystems: non-flooded upland areas (aerobic) and flood-prone lowland areas (anaerobic), with a pH between 5.5 and 6.5 (Fageria, Wander, and Silva, 2014; Infoagro, 2020). Given the low availability of Fe in soil, it requires the use of Strategies I and II for absorption (Petrik, Zhai, Haas, and Decristoforo, 2017; Yang, Li and Chen, 2020; Roskova, Skarohlid, and McGachy, 2022).

On the other hand, Mn in soil exists in a reduced form as Mn^{2+} (highly soluble and available), and in oxidized form as Mn^{3+} and Mn^{4+} (insoluble and unavailable) for plants (Navarro and Navarro, 2013; Haque et al. 2015; K.B. et al. 2023). The presence of Mn in soil is influenced by physical, chemical, and microbiological factors, with pH and redox conditions being the most significant (Husson, 2013). In acidic soils with a pH less than 5.5, Mn oxides solubilize and release Mn^{2+} into the soil solution (Millaleo, Reyes-Díaz, Ivanov, Mora and Alberdi, 2010; Herndon and Brantley, 2011).

On the contrary, water-soluble and exchangeable Zn constitute the fraction directly available for absorption, existing as free ions (Zn^{2+} and $ZnOH^+$), soluble organic complexes, and labile Zn (unstable) (Noulas, Tziouvalekas and Karyotis, 2018; Liu et al., 2020). The dominance of Zn^{2+} or $ZnOH^+$ depends on soil pH, with $ZnOH^+$ prevailing at pH above 7.7 and $Zn(OH)_2$ dominating at pH above 9.1 (Alloway, 2008; Kaur et al., 2024). It has been observed that in soils with a pH below 5.8, the exchangeable Zn fraction increases from organically complexed Zn (Yang et al., 2010).

Two mechanisms for micronutrient adsorption by clays and organic matter are apparent: one occurring in acidic conditions, related to cation exchange, and the other in alkaline conditions, involving chemisorption and the formation of complexes by organic ligands. In lowland or flood conditions, Zn availability in rice crops decreases due to the low redox potential, leading to the formation of non-exchangeable Zn complexes bound to clay particles. Additionally, in alkaline soils, free Zn precipitates as $Zn(OH)_2$, raising the pH, or as ZnS in sodic and calcareous soils (Sharma et al., 2013; Rose et al., 2013; Kaur et al. 2024).

Zinc absorption by plants occurs through mechanisms such as mass flow of passive nutrient transfer, diffusion near the roots (from the rhizosphere to the roots), and root interception within the soil profile.

It is transported to above-ground plant parts and intracellularly for metabolic processes (Bashir et al., 2012; Haroon and Khan, 2022). Key genes involved in Zn absorption are *OsZIP1* and *OsZIP3*, whilst those important to the translocation within

the root include *OsZIP4*, *OsZIP5*, *OsZIP8* (Bashir et al., 2012). Zinc translocation from the leaves to plant organs occurs through the symplast and apoplast via the xylem, with high levels of the micronutrient detected in the phloem (Liao et al. 2023; Marschner, 1995).

The Importance

Iron, Magnesium and Zinc play pivotal roles in the growth, development, and yield of rice. However, 50% of rice soils are deficient in Zn, and 30% are deficient in Fe (Ullah et al., 2017; Nadeem and Farooq, 2019). Iron plays a role in electron transport, redox systems, sulfur and nitrogen metabolism, DNA synthesis, hormone production, coenzymes, chlorophyll biosynthesis, and heme synthesis by ferrochelatase (Zhang et al., 2012; Wang et al., 2017; Ning et al., 2023). In upland areas with alkaline and calcareous soils, Fe levels below 50 mg kg^{-1} can cause nutritional disorders, and reduced productivity (Marschner, 2011; Rice Knowledge Bank, s.f.). In alkaline soils with high bicarbonate concentrations, the solubility and absorption of Fe, Mn and Zn decrease, especially in Strategy I plants, which rely on inducible ferric reductases for the cellular transport of Fe (Lucena et al., 2003; Zhang et al., 2019; Castilla and Tirado, 2019). In New Delhi, Kumar, Dinesh, Singh and Rishi (2015) found that foliar pulverization of 2.0% Fe sulfate in rice crops increased the yield (5.24 t ha^{-1} compared to the control's 4.32 t ha^{-1}). In Nigeria, Sakariyawo, Oyediji and Soretire (2020) obtained a yield of 196.40 g per plot in rice in upland areas with sufficient Fe (8.00 mg kg^{-1}), whereas in plants deficient in Fe (3.05 mg kg^{-1}), the yield was 10.00 g per plot.

Mn is an enzymatic activator in the Krebs cycle and in urea (arginase). It is involved in chlorophyll synthesis, is essential in the Mg-protein complex which transports electrons from the water to the photosystem II, and is part of Mn-SOD (Manganese superoxide dismutase)- an isoenzyme present in mitochondria and peroxisomes and, less frequently, in chloroplasts (Marschner, 2011; Grundmeier and Dau, 2012). The appropriate Mn level ranges from 30 to 600 mg kg^{-1} ; levels below 20 mg kg^{-1} cause interveinal chlorosis, short leaves, and atrophy (Rice Knowledge Bank, s.f.; Ullah et al., 2017).

This Mn deficiency is rarely seen in flooded rice. However, it has been observed in direct-seeded aerobic rice systems due to the oxidation of Mn^{2+} , a process which leads to the precipitation of Mn^{3+} and Mn^{4+} oxides. The application of Mn (0.02 mol l^{-1} Mn) in flooded and direct-seeded aerobic rice plants in Pakistan improved grain yield by 25.1% (Tao et al., 2007; Li et al., 2016). In China, it was found that the application of Mn in rice pots with sandy loam soil improved the rice quality. For early-season rice, the application of 1.100 mg of MnSO_4 resulted in 20.83% more panicles, and the application of 250 mg of MnSO_4 led to a weight increase of 12.96% in 1000 rice grains compared to the control (without Mn). Similarly, for late-season rice, the weight of 1,000 grains was 9.89% higher than the control, as found by Ullah et al. (2017).

Zinc is a micronutrient crucial for cytochrome synthesis, photosynthesis, phytohormone activity, and the metabolism of carbohydrates, nitrogen, lipids, and nucleic acids. It also plays a role in tryptophan and protein synthesis, as well as gene expression and regulation. Zinc stimulates enzymatic activities such as phosphatases and decarboxylases, contributes to the formation of flavonoid pigments and ascorbic acid, and serves as an auxin activator (Fageria, Dos Santos, and Cobucci, 2011; Saxena, Das, and Choudhury, 2017; Noulas, et al., 2018; Prakash, Sobhana, Sujithra and Hemalatha, 2019). The appropriate Zn level is 20 ppm. Levels below 10 mg kg^{-1} lead to red pigmentation in the lower leaves of plants, affecting flowering and anthesis. Leaf and root atrophy occurs, and grain yield reduces due to oxidative stress (Lee, Wissuwa, Zamora and Ismail, 2017; Gorain, Paul, and Parihar, 2022). In flooded conditions, rice's phosphate and bicarbonate concentrations increase, reducing Zn availability due to the low redox potential in the soil (Sharma et al., 2013; Prakash et al., 2019).

Fageria et al. (2011) reported a 97% higher increase in the grain yield in greenhouse-cultivated rice in Inceptisol soils in Brazil with 20 mg of Zn kg^{-1} compared to the control. Rengel, Cruz, Croce, Montaña and Chirinos (2012) reported a 63% increase in height and a 2.76% increase in rice grain weight following foliar application of Zn (350 g ha^{-1}). Ghoneim (2016) found that the applying

15 kg Zn ha^{-1} in the soil resulted in maximum plant height (100 cm) and the highest grain yield of 9.60 tons ha^{-1} . Utilizing Zn-solubilizing rhizobacteria is the most effective approach to correct Zn deficiency in a sustainable agricultural production system. Plant growth-promoting rhizobacteria (PGPR) colonize the rhizosphere and promote rice growth mechanisms (Pradhan et al., 2021).

Main Solubilizing Microorganisms for the Micronutrients Fe, Mn, And Zn in Rice Cultivation

Plant Growth-Promoting Bacteria (PGPR) such as *Bacillus*, *Pseudomonas* and *Azospirillum* promote the growth of rice plants and may possess properties that aid antibiosis and induction systematic resistance against pathogens.

Bacillus, a genus of Gram-positive bacteria from the Bacillaceae family, is rod-shaped and exhibits aerobic, or on occasion facultative anaerobic, growth. It thrives in neutral pH conditions and forms endospores, enabling survival in various extreme environmental conditions such as extreme temperature, pH, and salinity (Govindasamy et al., 2010). In crop rhizospheres, bacteria like *B. subtilis*, *B. licheniformis*, *B. megaterium*, and *B. pumilus* are commonly found (Griffiths, 2013; Tiwari et al., 2019).

Pseudomonas, a genus of polarized aerobic, Gram-negative rod-shaped bacteria from the Pseudomonadaceae family, exhibits optimal growth at a pH of 6 and a temperature of 30°C (Sivakamasundari and Usharani, 2012; Shruti, Arun, and Rai, 2013; Kumar et al., 2017; Meena et al., 2019).

Azospirillum, a rhizobacterium from the Rhodospirillaceae family, consists of curved Gram-negative rods. It is mobile via peritrichous flagella; strictly aerobic, and non-symbiotic nitrogen fixers that inhabit soil and easily adapt and grow in anaerobic, microaerobic, and aerobic conditions. *Azospirillum* thrives best at a pH between 6 to 8 (Botero, Castaño Zapata, and Saldarriaga, 2013).

Research indicates that rice plots treated with specific strains of *Pseudomonas Jesenii* (R62) and *Pseudomonas synxantha* (R81) at a concentration of 1×10^8 CFU showed improved Fe absorption,

resulting in an increased average rice seed yield of 22.66 g ton⁻¹ compared to the control yield of 15.61 g ton⁻¹. Conversely, rice plants inoculated with *Bacillus* sp. (14B) exhibited an average Fe concentration of 18.55 g ton⁻¹ in rice seeds, surpassing the control of average of 15.61 g ton⁻¹ (Gusain and Sharma; 2019).

Sharma, Shankhdhar & Shankhdhar (2013) in India, applied three standard PGPR strains (*Pseudomonas putida* MTCC 102, *Pseudomonas fluorescens* MTCC 103, and *Azospirillum lipoferum* MTCC 2694) to the roots of 21-day-old rice seedlings and found that the highest active Fe concentration was achieved with the inoculation of *Azospirillum lipoferum* in different rice genotypes. The Pusa basmati-1 genotype exhibited the highest concentration at 25.30 (µg g⁻¹ DW) compared to the control's 14.39 (µg g⁻¹ DW).

In Brazil, it has been reported that *Bacillus* sp. applied at a concentration of 1 x 10⁸ CFU is the main Zn-solubilizing microorganism (Nascente et al., 2017). In Pakistan, *Bacillus* sp. SH-10 and *Bacillus cereus* SH-17 at a concentration of 1x10⁹ CFU (Shakeel et al., 2015); in India, *Pseudomonas aeruginosa* at a concentration of 1 x 10⁹ (Gontia-Mishra et al., 2017), *Pseudomonas fluorescens* and *Pseudomonas aeruginosa* at a concentration of 1 x 10⁶ (Gontia-Mishra et al., 2016), as well as *Pseudomonas putida* MTCC 102, *Pseudomonas fluorescens* MTCC 103, and *Azospirillum lipoferum* MTCC 2694 at a concentration of 1 x 10⁷ CFU (Sharma et al., 2014).

Furthermore, they report on *Pseudomonas jessenii* in combination with *Pseudomonas synxantha* (R62 + R81) and *Bacillus* sp. (14B) at a concentration of 1 x 10⁸ CFU. In Pakistan, in the roots of basmati-385 rice and in basmati from clayey and saline soil, 234 isolates of *Bacillus* sp. were obtained at a concentration of 1x10⁹ CFU, of which 27 solubilized Zn minerals, such as Zn phosphate, carbonate, and oxide. *Bacillus* SH-10 had the largest solubilization zone of 24 mm with Zn phosphate. *Bacillus cereus* SH-17 achieved a maximum solubilization of 15 mm with Zn oxides and carbonates. *Bacillus* sp. and *Bacillus cereus* improved Zn translocation to the grains and increased the

yield of the mentioned varieties from 18% to 49% (Shakeel, Rais, Hassan & Hafeez, 2015).

Pseudomonas aeruginosa has shown Zn solubilization greater than 10 mm in supplemented media, probably due to the production of organic acids such as gluconic acid, 2-ketogluconic acid, 5-ketogluconic acid, and pentanoic acids (Gontia-Mishra et al., 2016; Gontia-Mishra et al., 2017; Gusain & Sharma 2019). In India, it was found that the application of *Pseudomonas jessenii* (R62) and *P. synxantha* (R81) at a concentration of 1 x 10⁸ CFU to rice varieties Swarna, Swarna sub1, IR-64, and IR-64 sub1 twice at the time of seed sowing, and transplanting significantly affected Zn absorption, resulting in a micronutrient content in rice seeds of 22.75 g ton⁻¹ compared to the control's 16.60 g ton⁻¹. The same authors determined that the Mn concentration in rice seeds was higher at 26.66 g ton⁻¹ with the application of *P. jessenii* (R62) and *P. synxantha* (R81).

Nascente et al. (2017) found greater Fe and Mn absorption in rice seeds inoculated with *Pseudomonas* sp. at a concentration of 1 x 10⁸ CFU, obtaining 169 mg Kg⁻¹ and 2190 mg Kg⁻¹ compared to the controls' 122 mg Kg⁻¹ and 1.864 mg kg⁻¹, respectively. Similarly, seeds inoculated with *Bacillus* sp. had the highest Zn content at 48 mg Kg⁻¹ compared to the control's value of 43 mg Kg⁻¹. Ikhajagbe & Ohanmu (2019) found that after 13 weeks of applying *Bacillus subtilis* and *Pseudomonas aureginosa* at a concentration of 1.52 x 10⁵ CFU/g to rice plants, the yield growth increased by 0.53 g compared to that obtained by the control, 0.28 g.

Characteristics And Main Use of Bacterial-Based Biofertilizers Promoting Fe, Mn, And Zn Nutrition

Utilizing biofertilizers containing *Bacillus* sp., *Pseudomonas* sp., and *Azospirillum* sp. represents a promising approach to achieving optimal crop nutrition while maintaining environment integrity (Velasco Sánchez, Delgado García, and Moreno Lora, 2017). *Bacillus* bacteria, belonging to the Bacillaceae family, are Gram-positive bacteria aerobic or facultative anaerobic growth. They thrive in neutral pH environments and can

withstand extreme temperature and pH conditions, including saline conditions (Griffiths, 2013; Tiwari, Prasad & Lata, 2019). Common species include *B. subtilis*, *B. licheniformis*, *B. megaterium*, and *B. pumilus* (Tiwari et al., 2019; Tiwari, Prasad and Lata, 2019).

Pseudomonas, a genus of MIGULA (1894) found that Gram-negative bacteria of the Pseudomonadaceae family, have approximately 191 diverse species (Anzai, Kim, Park, Wakabayashi and Oyaizu, 2000; Sankari Meena et al., 2019). These bacteria exhibit optimal growth conditions at a pH of 6 and a temperature of 30°C (Kumar et al., 2017; Sankari Meena et al., 2019; Shruti K, Arun K, 2013).

Azospirillum, a genus of bacteria from the Rhodospirillaceae family, comprises Gram-negative bacilli capable of thriving under anaerobic, microaerobic, and aerobic conditions. They exhibit optimal growth at a pH range of 6 to 8 (Botero, Castaño Zapata, and Saldarriaga, 2013).

An agricultural inoculant for the solubilization of soluble micronutrients in soil for promoting the production of physiologically active substances is a consortium of *Bacillus licheniformis* (7×10^9 CFU mL^{-1}), *Bacillus subtilis* (6×10^9 CFU mL^{-1}), and *Pseudomonas fluorescens* (7×10^9 CFU mL^{-1}). Biofertilizers containing *Bacillus megaterium* (1×10^8 CFU mL^{-1}) exhibit direct phytohormonal action on crop growth and productivity, favoring the absorption of minerals such as Fe, Mn, and Zn, as well as solubilizing macronutrients like phosphorous. Similarly, biofertilizers with *Pseudomonas* sp. (1×10^8 CFU mL^{-1}) enhance growth and yields (Kumar, Meena & Singh, 2016). *Pseudomonas fluorescens* also improves yield and provides biological control over pathogens through siderophores production.

Azospirillum sp. (7×10^8 CFU mL^{-1}) serves as a biological inoculant promoting plant growth when applied to soil or seeds. *Azospirillum brasilense* M3 (1×10^8 CFU mL^{-1}) supplies plants with essential N-P-K nutrients, stimulates phytohormones production, and fosters plant growth (Pereg, de-Bashan, & Bashan, 2016). In rice cultivation, *Azospirillum brasilense* (1×10^9 CFU mL^{-1}) stimulates the synthesis of indole-3-acetic acid (IAA) and plant growth regulators such as gibberellins, cytokinins, and ethylene (Bashan & de-Bashan, 2010).

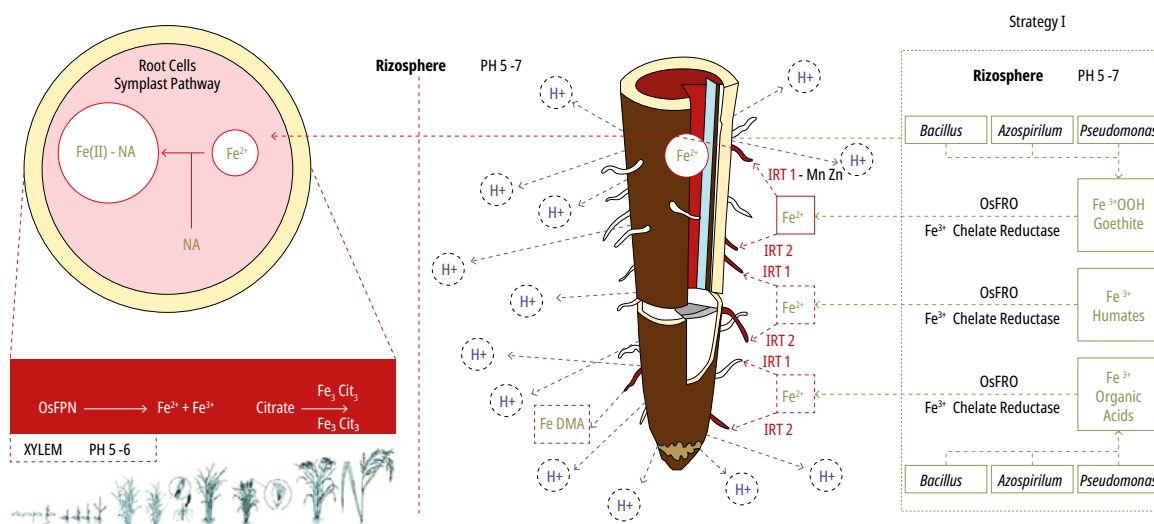
Commercially available under various brand names, *Bacillus* sp., *Pseudomonas* sp., and *Azospirillum*-based biofertilizers are offered alone or in mixtures tailored for rice cultivation in countries such as Mexico, Colombia, and Spain (Portal Tecnológico, 2023; Organización Pajonales SAS, 2023; ICA, 2023).

Mechanisms Involved in the Solubilization of The Micronutrients by the Microorganisms *Bacillus*, *Pseudomonas*, and *Azospirillum*

To address (Fe) deficiency in calcareous soils, rice employs Fe absorption mechanisms that integrate two strategies within a specialized system (Ishimaru et al., 2006; Kar & Panda, 2020). However, this crop can adapt to conditions where Fe^{2+} is more prevalent than Fe^{3+} (Aguado-Santacruz et al., 2012). In strategy I, first, protons (H^+) are released from the root plasma membranes, acidifying the soil and enhancing the solubility of Fe^{3+} . Secondly, the activity of ferric reductase-oxidase (OsFRO) enhances the ability to reduce chelated iron III (Fe^{3+}) to iron (II) Fe^{2+} on the root surface. Thirdly, Fe^{2+} is absorbed across the root plasma membrane, reduced by Fe(III) chelate reductase encoded by genes (iron transporters) IRT1 and IRT2, which encode Fe(II) transporters. Moreover, the IRT1 gene is responsible for Zn and Mn absorption as well (Ishimaru et al., 2006; Marschner, 2011; Wairich et al., 2019; Kar & Panda, 2020; Ning et al., 2023). (Refer to Figure 1).

Wairich et al. (2019) demonstrated that *Bacillus subtilis* GBO3 acidifies the rhizosphere and activates strategy I's Fe absorption responses, resulting in a high content of endogenous plant iron. *Bacillus subtilis* bacteria can directly activate strategy I for Fe acquisition in *Arabidopsis thaliana* plants without colonizing the plant's roots. This mechanism is attributed to the production of volatile organic acids by the microorganism (Aguado-Santacruz et al., 2012).

In strategy II (refer to Figure 2), rice plants synthesize and excrete phytosiderophores (ps) of the mugineic acid (MA) family, derived from deoxymugineic acid (DMA), to chelate Fe^{3+} into Fe^{3+}PS

Figure 1. Procedure for Iron Uptake, Symplastic Transport, and Xylem Transport in Rice

Source: Adapted from Ariga *et al.* (2014).

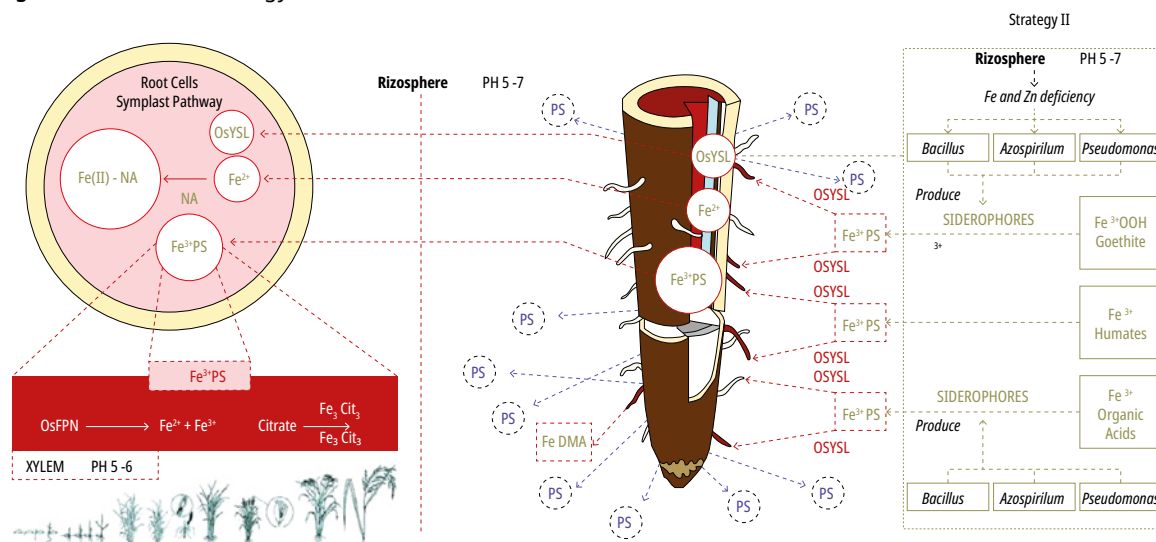
complexes in the plant root through the OsYSL15 protein. The OsYSL9 protein is possibly responsible for transporting Fe (III)-DMA and Fe (II)-nicotianamine (NA) into the endodermis of the root (Inoue *et al.*, 2009; Nozoye *et al.*, 2011; Senoura *et al.*, 2017; Kawakami & Bhullar, 2018; Q. Wu *et al.* 2022). Internal translocation of Fe and Mn to the shoots and seeds is facilitated by the OsYSL2 protein. Meanwhile, regarding Mn transport and regulation in rice, there is limited research (Ishimaru *et al.*, 2010; Petrik, Zhai, Haas, and Decristoforo, 2017). In rice plants with low Fe concentrations, both deoxymugineic acid (DMA) and mugineic acid (MA) were found, with PS (μM) and Fe (μM) concentrations ranging from 0.49 μM (Nozoye *et al.*, 2011; Ariga, Hazama, Yanagisawa, and Yoneyama, 2014). The release of PS, akin to the uptake of Fe^{3+} -PS complexes by the plant, occurs after exposure to the first light rays, where the complex enters the cytoplasm through Fe^{3+} -PS transporters attached to protons on the plasma membrane of root cells (Ishimaru *et al.*, 2006).

Under conditions of Fe and Zn deficiency, microorganisms synthesize and secrete low molecular weight Fe-chelating proteinaceous siderophores of the catecholate, hydroxamate, phenolate, and carboxylate types to enhance the availability of Fe^{2+} and transport across the plant cell membrane

(Kumar *et al.*, 2017; Hofmann, Retamal-Morales, and Tischler, 2020; Roskova *et al.*, 2022).

Das, Prasad and Srivastava (2007) reported the large-scale synthesis of siderophores in species such as *Bacillus*, *Pseudomonas*, *Azospirillum*, among others. *Bacillus megaterium* has the capacity to produce siderophores (Santos, Neto, Machado, Soares, & Soares, 2014). Siderophores are synthesized from L-methionine and involve enzymes such as S-adenosylmethionine synthetase, nicotianamine synthase, nicotianamine aminotransferase, and desoximugineic acid synthase (Roskova *et al.*, 2022). The synthesis of siderophores in rice plants was initially studied by Takagi (1976). Bacterial siderophores, like pyoverdine produced by *Pseudomonas fluorescens*, exhibit high affinity for iron (Yehuda *et al.*, 1996; Bonneau, Roche & Schalk, 2020).

The availability of Mn in the soil varies and depends on numerous environmental and biotic soil factors. Plants require Mn^{2+} at a much higher concentration than fungi and bacteria (Marschner, 1995, Khoshru *et al.*, 2023). Many bacteria have sophisticated mechanisms for coordinating the detection of Mn and the responding to oxidative stress. For instance, *Bacillus subtilis* possesses a coordinated network of metalloproteins, including a Fe^{2+} uptake regulator (plasma membrane), an

Figure 2. Process of Strategy II in Rice

Source: Adapted from Ariga *et al.* (2014).

Mn^{2+} transport regulator (MntR), and a $\text{Fe}^{2+}/\text{Mn}^{2+}$ peroxide regulator repressor (PerR) of genes. This network regulates intracellular concentrations of Fe^{2+} and Mn^{2+} , detects H_2O_2 concentrations, and ultimately controls, through PerR, oxidative stress response genes (Herbig and Helmann, 2001; Sieprawska *et al.* 2024).

Zinc-solubilizing bacteria employ specific mechanisms to transform insoluble forms of Zn into soluble forms that are easily absorbed by plants. They achieve this through chelation, forming chelating compounds by binding with Zn, and through acidification, producing organic acids that reduce the soil pH, thereby facilitating the mobilization of Zn and improving root growth and absorption area (Neumann and Römhelt, 2002; Subramanian, Tenshia, Jayalaskshmi, Ramach and Ran 2009). In such cases, the PGRP group of bacteria, especially *Bacillus* sp. and *Pseudomonas fluorescens*, demonstrate Zn solubilization across a wide range of Zn minerals. Additionally, *Bacillus megaterium* and *Bacillus edaphicus* increase Zn availability in the soil. These mechanisms also involve the secretion of root chemical exudates, providing an additional benefit to the solubilization process

of this micronutrient (Maheshwari, 2012). For example, *Pseudomonas fluorescens* secretes gluconic and 2-ketogluconic acids into the rice crop during Zn phosphate solubilization (Di Simine, Sayer & Gadd, 1998). Some Zn solubilization mechanisms function via the production of indole-3-acetic acid (IAA), as determined by growing microorganism strains like *Pseudomonas* on LB agar plates supplemented with $100 \mu\text{g mL}^{-1}$ of tryptophan (Shrivastava and Kumar, 2011). Additionally, anions can chelate Zn and enhance its solubility (Jones & Darrah, 1994). Other mechanisms in Zn solubilization include the production of siderophores (Saravanan *et al.*, 2011b; Northover *et al.* 2021), oxidoreductase systems in cell membranes, and chelating ligands (Singh *et al.*, 2012). Strains of *Bacillus* sp. and *Bacillus cereus* have been found to enhance the translocation of Zn and other nutrients to the grains, thereby increasing rice variety yields (Shakeel *et al.*, 2015; Barbosa *et al.*, 2023).

The various mechanisms mentioned for the solubilization of the micronutrients Fe, Mn and Zn, associated with microorganisms *Bacillus*, *Pseudomonas* and *Azospirillum*, are presented in Table 1.

Table 1. Different mechanisms involved in the solubilization of the micronutrients Fe, Mn and Zn by the microorganisms *Bacillus*, *Pseudomonas* and *Azospirillum*.

Genus and species of microorganism	Mechanisms of action			References
	Fe	Mn	Zn	
<i>Bacillus</i> : B. sp.(1), <i>B. subtilis</i> (2), <i>megaterium</i> (3), <i>B. sp. B. megaterium</i> y <i>B. edaphicus</i> .(4) <i>B. sp. y B. cereus</i> (5) <i>B. subtilis</i> , <i>B.</i> <i>licheniformis</i> , <i>Azospirillum</i> (6)	Strategy II y Strategy II (1) secreción siderophore secretion of Fe (1), (2), (3), (5) Solubilization of Fe (1), (5), (6)	Solubilization of Mn (1), (3), (5), (6)	Solubilization of Zinc (1), (3), (4), (5), (6) siderophore secretion (4), (5)	Herbig & Helmann, 2001; Ishimaru et al., 2006; Das et al., 2007; Inoue et al. 2009; Nozoye et al., 2011; Marschner, 2011; Maheshwari, 2012; Aguado-Santacruz et al., 2012; Srivastava et al., 2013; Santos et al., 2014; Ariga et al., 2014; Shakeel et al., 2015; Kumar et al., 2017; Senoura et al., 2017; Kawakami & Bhullar, 2018; Wairich et al., 2019; Hofmann et al., 2020; Kar et al., 2020; Panda, 2020; Roskova et al., 2022; Q. Wu et al. 2022; Barbosa et al., 2023; Ning et al., 2023; Sieprawska et al. 2024; ICA, 2020. www.ica.gov.co
<i>Pseudomonas</i> : <i>P. fluorescence</i> (1), <i>P. putida</i> MTCC 102 y <i>P. fluorescens</i> MTCC 103 (2), <i>P. sp</i> (3), <i>P. aeruginosa</i> y <i>P. fluorescens</i> (4), <i>P. jessenii</i> en combinación con <i>P. synxantha</i> (R62 + R81) (5), <i>P. sp.</i> (6)	Solubilization of Fe (2),(5), (6)	Solubilization of Mn (2), (6)	Solubilization of Zn phosphate. (Chelating Compounds) (1) Solubilization of Zinc (2), (4), (6) siderophore secretion (2)	Santos et al., 2014 Roskova et al., 2022 Saravanan et al. 2007; Northover et al. 2021; Shakeel et al., 2015; Meena et al., 2016 Gontia-Mishra et al., 2017 Bapiri et al., 2012 & Gontia-Mishra et al., 2016; Gontia-Mishra et al., 2017 Gusain & Sharma, 2019; Sharma et al., 2014 Sharma et al., 2014 Shakeel, Rais, Hassan, & Hafeez, 2015 Maheshwari, 2012 Di Simine, Sayer & Gadd, 1998
<i>Azospirillum</i> : <i>A. lipoferum</i> MTCC 2694 (1) <i>A. brasilense</i> M3 (Bulhnova), <i>A. brasilense</i> (2) <i>Azospirillum</i> sp. Dimazos SC (3)	Siderophore production (1)		Solubilization of Zn (1), (2),	Santos et al., 2014 Roskova et al., 2022 Sharma et al., 2014; Sharma et al., 2013 Flores et al., 2010; Del Amor & Cuadra, 2011; Schoebitz, Mengual, & Roldán, 2014 https://www.probelte.es/productos/detalle/es/bulhnova/137 https://www.buscador.portaltecnogagricola.com/vademecum/esp/producto/KIPLANT%20iNmass ICA, 2020. www.ica.gov.co ; Maheshwari, 2012 El-Sayed et al., 2014; Sharma et al., 2014; Abaid-Ullah et al., 2015

Discussion

The microorganisms *Bacillus*, *Pseudomonas*, and *Azospirillum* exert an effect on the availability of Fe, Mn, and Zn in calcareous soils for rice cultivation by secreting siderophore compounds that

absorb micronutrients in the form of chelates through plant roots. *Bacillus megaterium*, *Pseudomonas putida*, *P. fluorescens*, and *P. aeruginosa* are commonly reported as producers of siderophores and for transporting minerals internally to plant cells, thereby enhancing crop nutrition (Das et al.,

2007; Aguado-Santacruz et al., 2012; Srivastava, 2013; Sharma et al., 2014; Santos, 2014; Shakeel et al., 2015; Gusain & Sharma, 2019). However, Ariga et al. (2014) attribute the solubilization of unavailable micronutrients to phenols or aromatic compounds. Ishimaru et al. (2006) mention that carrier genes are required by plants to transport chelated minerals for micronutrient absorption, as seen with *Bacillus subtilis*, whose oxidative stress genes regulate Fe^{2+} and Mn^{2+} (Herbig & Helmann, 2001). Consequently, it can be inferred that these microorganisms contribute to micronutrient assimilation, not only through Siderophore production but also through the synthesis of phenols and other plant growth-promoting substances such as indole acetic acid, abscisic acid, and cytokinins (Nautiyal, 2016; Tiwari & Singh, 2017; Vimal et al., 2019).

When these microorganisms are applied in rice cultivation, they positively impact the panicles plant height, tillers numbers, and grain size and weight (Shakeel et al., 2015; Meena et al., 2016; Gontia-Mishra et al., 2017; Nascente et al., 2017; Yang, 2020). These mechanisms, at a biochemical level, may involve enzymatic reactions, influencing plant growth-promoting substances, thereby affecting rice plant and grain formation (Noulas et al., 2018; and Prakash et al., 2019). Additionally, environmental and edaphic conditions play a crucial role in plant development and grain quality. In this way, the concentrations of minerals such as Fe, Mn and Zn the depend on pH (between 5 and 7), soil texture, rice genetics, and crop nutrition (Marschner, 2011; Shakeel et al. 2015; Ullah et al., 2017; Gontia-Mishra et al., 2017; Infoagro, s.f).

In the market, registered biofertilizers containing *Bacillus*, *Pseudomonas*, and *Azospirillum* (Dimazos® SC-Biocultivos S.A., Bulhnova-Probelte, S.A.U, Kiplant iNmass®- Portal Tecnoagrícola, Fosfobacter®- Organización Pajonales SAS, Actifos SL Mycros®-Agro Valley SAS) have demonstrated favorable results in solubilization Fe, Mn and Zn micronutrients and can be used in rice agriculture.

However, further research is recommended on the application of *Pseudomonas* and *Bacillus* as biofertilizers to enhance Mn solubilization in

rice cultivation, given its significance as a micro-nutrient for crop yield. The majority of research on these microorganisms focuses in solubilizing micronutrients Fe and Zn (Noulas, et al. 2018; Prakash et al. 2019). Similarly, expanding knowledge on azospirillum application is suggested, as it is the least mentioned genus of plant growth-promoting, when compared with pseudomonas and bacillus for the solubization of Fe, Mn in the aforementioned crops.

Conclusions

Iron, Mn, and Zn solubilizing microorganisms from the genera *Bacillus*, *Pseudomonas*, and *Azospirillum* have been extensively utilized in rice cultivation across various countries including India (53%), Pakistan (13%), Brazil (7%), China (7%), Egypt (7%), Iran (7%), and Belgium (6%). The inoculation of *Bacillus*, *Pseudomonas*, and *Azospirillum* bacteria into rice varieties grown in calcareous soils with limitation in Fe, Mn, and Zn facilitates the availability of these micronutrients and the formation of siderophores by the plants. This process promotes soil acidification and aids in converting non-assimilable forms into soluble ones, thereby enhancing rice's metabolic and enzymatic processes, ultimately leading to improved crop development, yield, and grain quality.

Globally, more research has been conducted on *Pseudomonas* and *Bacillus* for the solubilization of Fe and Zn minerals compared to Mn, where fewer experiments in rice cultivation have been identified. *Azospirillum*, on the other hand, is less frequently utilized for Fe, Mn, and Zn fertilization. The utilization of these bacteria holds promise for increasing rice yield, quality, and productivity while mitigating negative environmental impacts associated with synthetic fertilizers.

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