



REVIEW ARTICLE

Zinc-solubilising rhizobacteria bioformulations in rice systems: Mechanisms, bioformulation strategies and implications for long-term soil health and nutrient

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Abstract

Zinc (Zn) deficiency in soils poses a serious threat to global food and nutritional security, especially in developing countries where unsustainable farming, like imbalanced fertiliser use, nutrient mining and organic matter loss, is widespread. In India, surveys of over 242000 soil samples across 615 districts reveal widespread micronutrient deficiencies: 51.2 % for Zn, 58.6 % for sulfur (S) and 44.7 % for boron (B). Common combined deficiencies such as Zn + S (9.3 %), Zn + B (8.7 %) and Zn + iron (Fe) (5.8 %) vary spatially across agro-ecological zones. These findings highlight the urgent need for site-specific integrated nutrient management tailored to diverse soils and crops. Conventional Zn biofortification methods using ZnSO₄ or Zn-chelates have shown benefits but face limitations including high costs, poor adoption and reduced efficacy in acidic soils prevalent in eastern India. Alternatively, microbiological biofortification with Zn-solubilising bacteria (ZSB) offers a sustainable, low-cost solution. ZSB transform insoluble Zn into plant-available forms through mechanisms like chelation, organic acids and siderophore production, enhancing Zn uptake, grain quality and yield. This approach supports sustainable agriculture by improving nutrient use efficiency, reducing chemical inputs and promoting soil microbial health. In acid soils of Odisha, deploying effective ZSB strains offers a promising route to improve soil fertility and combat hidden hunger by boosting micronutrient content in crops. This review synthesises current understanding of ZSB-mediated Zn mobilisation and their application in sustainable Zn biofortification of rice-based systems, particularly in Zn-deficient regions and highlights key research priorities for translating laboratory insights into reliable field-scale outcomes.

Introduction

Zinc (Zn) is an essential micronutrient in plants, functioning as a catalytic, structural and regulatory cofactor in over 300 enzymatic processes. These enzymes govern vital physiological pathways, including carbohydrate metabolism, protein biosynthesis and nucleic acid regulation. Beyond its metabolic roles, Zn is indispensable for chlorophyll synthesis and efficient photosynthesis, crucial processes driving vegetative growth. Additionally, Zn regulates the biosynthesis of auxins such as indole-3-acetic acid (IAA), which are pivotal for root development, cell division and overall plant architecture. Deficiency in Zn manifests as chlorosis, stunted growth and distorted leaf morphology, particularly in early crop stages, ultimately reducing yield potential, especially in sensitive cereals like rice (1).

Despite its critical role, Zn deficiency remains a widespread agricultural challenge globally and is especially pronounced in India. National soil health surveys indicate that 45–50 % of Indian arable lands are deficient in available Zn (2). Several factors contribute to this problem, including intensive cropping systems that deplete micronutrient reserves, excessive reliance on Nitrogen, Phosphorus and Potassium (NPK) fertilisation and declining soil organic matter. The problem is exacerbated in specific soil types, acidic, red and lateritic soils prevalent in eastern and southern India, which are inherently prone to micronutrient leaching, nutrient fixation and low Zn bioavailability (3). In South and Southeast Asia, for instance, flooded rice systems dominate and the anaerobic conditions common in such environments drastically alter microbial dynamics and nutrient availability. Studies in Bangladesh and Vietnam (4) demonstrate that zinc-solubilising bacteria (ZSB) performance is constrained under reduced oxygen conditions, necessitating the

selection of facultative anaerobic strains capable of functioning in waterlogged soils. In contrast, in aerobic upland rice systems, such as those practised in Sub-Saharan Africa and some parts of South India, aerobic ZSB strains show better colonisation, survival and solubilisation efficacy (6).

Moreover, ZSB performance is strongly influenced by soil pH and mineralogy. In alkaline calcareous soils, such as those prevalent in the Mediterranean, Middle East and parts of northern India and China, carbonate-bound Zn is poorly soluble. ZSB isolated from these regions often demonstrate high efficiency in secreting gluconic acid, oxalic acid and siderophores to mobilise Zn (6). In contrast, ZSB from acidic lateritic soils such as those in tropical Africa, Brazil, or eastern India must be adapted to low organic matter content and high leaching potential, emphasising the importance of strain-specific adaptation (7). Notably, few studies have explicitly contrasted ZSB performance in flooded vs. aerobic rice systems or acidic vs. alkaline soils using the same microbial strains. Such comparative studies are essential for developing core vs. niche-specific ZSB inoculants. Furthermore, international field trials using meta-analytical frameworks could offer valuable insights into effect sizes and the context-dependency of ZSB efficacy under diverse farming systems. Additionally, the climatic regime plays a critical role. In temperate climates like parts of Europe or North America, microbial activity is subject to seasonal dormancy. The ZSB consortia in such regions require cold-tolerant traits and may benefit from encapsulation or carrier-based formulations to ensure persistence during off-seasons (8).

Odisha exemplifies this crisis, with over 70 % of its cultivable area dominated by acidic soils. Districts such as Rayagada, Koraput and Kandhamal face acute Zn deficiencies due to chemical fixation and soil pH-dependent reactions that render Zn unavailable, even when total Zn content appears adequate. Compounding the issue is the inefficiency of conventional Zn fertilisation: studies estimate that 96–99 % of applied Zn rapidly becomes unavailable to plants due to adsorption, precipitation, or complexation reactions (9). Consequently, traditional Zn supplementation strategies have often failed to address plant demand sustainably. Recent research highlights the promise of ZSB as biofertilizers capable of transforming insoluble Zn compounds into plant-available forms. These beneficial rhizospheric microbes employ mechanisms such as proton extrusion, organic acid secretion, siderophore production and redox transformations to mobilise Zn. Additionally, ZSB contribute to plant growth promotion through the synthesis of phytohormones, antimicrobial metabolites, siderophores and extracellular enzymes, enhancing nutrient uptake and stress resilience (10). Field applications of effective ZSB strains have demonstrated substantial improvements in crop biomass and yield under Zn-limiting conditions across cereals like rice, wheat and maize.

However, despite growing interest, critical knowledge gaps remain. There is limited region-specific data on the biodiversity, adaptability and solubilization potential of native ZSB strains, particularly in acidic, Zn-stressed soils of Odisha. Understanding the ecological interactions between indigenous microbial communities and introduced ZSB inoculants is essential for developing contextually appropriate biofertilizers. Moreover, research must focus on integrated nutrient management (INM) frameworks, combining microbial inoculants with organic amendments and optimised mineral fertilisation, validated through large-scale field

trials. This review summarises current knowledge on the role of Zn in crop physiology, the causes of Zn deficiency in Indian soils with emphasis on Odisha and the potential of ZSB as sustainable alternatives to conventional Zn fertilisers. It examines soil and agronomic factors influencing Zn deficiency, microbial mechanisms of Zn solubilization and research gaps in plant-microbe interactions and integrated nutrient management. The review also highlights priorities for developing eco-friendly Zn biofortification strategies to boost crop yield, soil health and nutritional security.

Zinc deficiency in soils for sustainable farming

Soil types susceptible to Zinc deficiency

Zinc has emerged as the fourth most critical yield-limiting nutrient in Indian agriculture. The incidence of Zn deficiency in Indian soils is projected to rise significantly to approximately 63 % by 2025 (Fig. 1). Despite India having the largest area under groundnut cultivation globally, it continues to lag behind China in total production, primarily due to lower productivity levels. While rainfed cultivation systems contribute to this yield gap, inadequate mineral nutrition, especially Zn, plays a decisive role. Among all nutrients, Zn deficiency alone can lead to yield reductions of up to 40 % in groundnut, underscoring its essential role in enhancing productivity (11). There are different types of soil in Odisha, which are a big reason why Zn deficiency is different in different parts of the state. Lateritic, red and acidic soils are the most affected by Zn deficiency. These types of soil are common in the southern and western districts.

Odishas' lateritic soils have been weathered a lot, have low nutrient levels, high levels of iron and aluminium oxide and not enough organic matter. These traits make Zn stick to things and hold on to them better, which makes it harder for crops to get to (12). Red soils, prevalent in tropical and subtropical regions, are typically acidic, possess a low cation exchange capacity (CEC) and exhibit poor retention of micronutrients. Acidic soils impede Zn availability for plants, as Zn ions tend to form insoluble compounds or adhere to soil particles, hence reducing their mobility and uptake by plant roots (13). Intense precipitation and leaching frequently exacerbate the acidity of these soils, hence diminishing the availability of Zn. Additionally, these soils typically exhibit low organic carbon content, complicating Zn uptake by plants. Low organic carbon reduces the formation of soluble organic-Zn complexes, which normally enhance Zn mobility and plant availability.

Zinc deficiency in Odisha

Extensive soil micronutrient assessments have revealed that Zn deficiency is not uniformly distributed; rather, it is concentrated in specific areas of Odisha (Fig. 2). The Soil Testing Laboratory of the Government of Odisha identified Rayagada, Koraput, Kandhamal, Keonjhar, Mayurbhanj and Malkangiri as regions with deficient Zn levels. Rayagada and Koraput districts have a significant deficiency of Zn, with more than 60–70 % of soil samples displaying DTPA-extractable Zn concentrations below 0.6 mg kg⁻¹, the threshold requisite for rice cultivation (14–16). The soils in Koraput and Kandhamal, located in the tribal-dominated hill regions, contain significant amounts of iron and aluminium oxides that effectively retain Zn. This is made worse by the fact that there isn't much organic matter and high-phosphate fertilisers are often used, which makes Zn less available. The red, acidic soils of Keonjhar and Mayurbhanj districts also make it hard for crops to get Zn, which

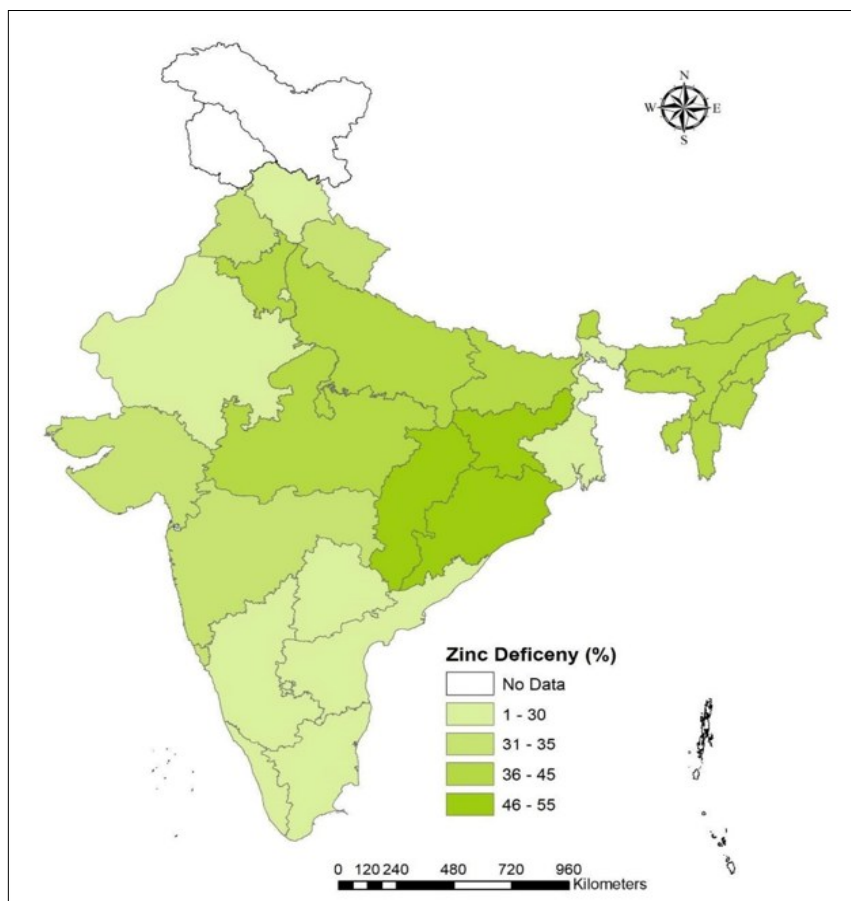


Fig. 1. Zinc deficiency throughout different states of India.

Source : ArcGIS, version 10.2.2.3552.

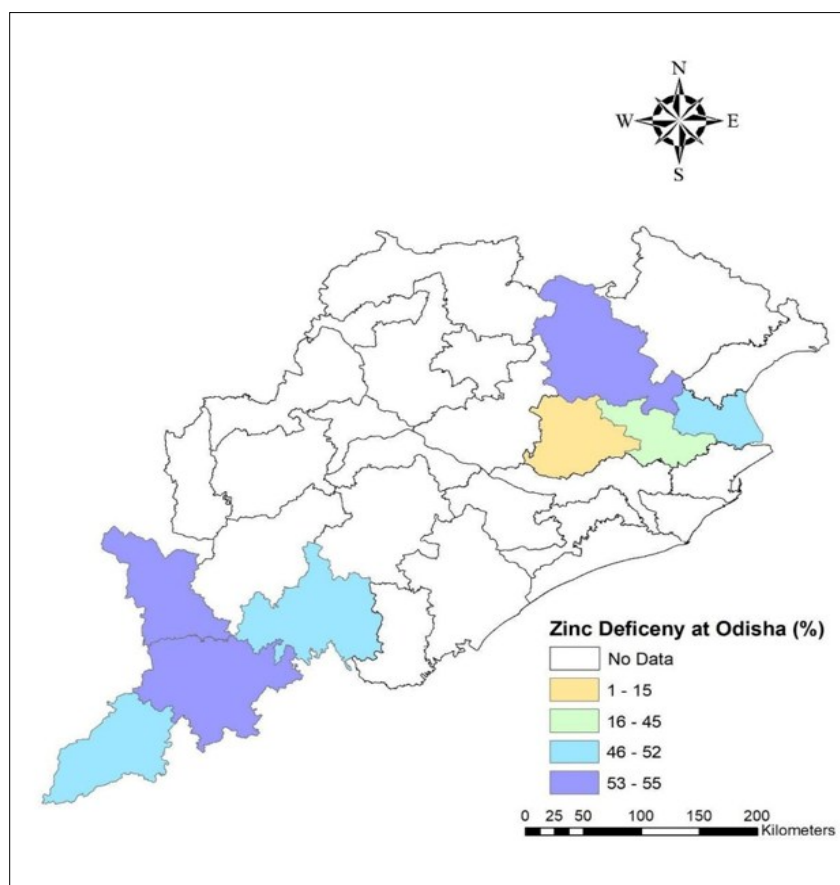


Fig. 2. Zinc deficiency throughout different districts of Odisha.

Source : ArcGIS, version 10.2.2.3552.

hurts their yields. These areas with low Zn levels often have lower crop yields and poor crop health indicators like chlorosis and stunted growth. This shows how important it is to have specific Zn management plans in place right away (Table 1).

Influence of soil physical and chemical properties on zinc availability

Soil chemical properties, especially pH, organic matter content and nutrient interactions, strongly influence Zn availability in soils. Zinc solubility is very dependent on soil pH. In acidic soils (pH < 5.5), Zn is usually more soluble, but it can stick to iron and aluminium oxides, making it less available to plants (17, 18). In alkaline soils, on the other hand, Zn forms insoluble hydroxides and carbonates, which plants can't use. Odishas' acidic soils are a difficult problem because Zn ions tend to get stuck in the soil instead of staying in the solution.

Organic matter is important for Zn nutrition in two ways. It makes the soil better by making it hold more water and improving its structure. It also helps with Zn chelation by making soluble organo-metal complexes that make Zn more mobile and available to plants (19, 20). But the low levels of organic matter in Odishas' Zn-deficient soils make this good effect less strong. The incorporation of organic amendments such as compost and green manure can improve Zn availability by increasing soil organic carbon and enhancing microbial activity.

Phosphorus–zinc interactions in soil systems

In several regions of Odisha, the excessive application of phosphate fertiliser is prevalent to enhance agricultural production. This may exacerbate Zn insufficiency. Phosphate ions interact with water-soluble Zn to form water-insoluble Zn phosphate complexes. This complicates Zn absorption by plants, despite adequate Zn availability in the soil (21, 22). To maintain optimal levels of P and Zn in the soil for superior crop nutrition, the antagonistic interaction necessitates meticulous management of fertilisers.

Performance of zinc-solubilising bacteria in aerobic and flooded rice systems

The redox state of the soil, which differs greatly between flooded (anaerobic) and aerobic rice cultivation systems, is a major determinant of ZSB inoculant efficiency. Comparative research shows that applying the same microbial strains under various water regimes results in differences in crop response and Zn solubilisation. Using the *Pseudomonas fluorescens* strain in both flooded and aerobic rice systems, research was carried out on a comparative field experiment in Bangladesh (23). Due to improved root oxygenation and microbial respiration, Zn uptake rose by 29.7 % in aerobic fields while only 14.3 % in flooded fields. Similar trends were seen in grain yield improvements, which increased by 7.2 % in flooding and 14.1 % in aerobic conditions. *Bacillus megaterium* produced fewer siderophores and organic acids in flooded paddy soils than in

aerobic soils, resulting in decreased Zn availability and uptake (24). This decrease was about 30 %. According to the study, ZSB activity is decreased in submerged conditions by oxygen limitation and modified rhizospheric pH buffering. *Azospirillum* sp. strain Zn-14 was tested under two irrigation schedules (25). Under aerobic conditions, the Zn content of grains rose by 11.6 %, while under flooded conditions, it increased by 6.8 %. In aerobic systems, soil enzymatic activities (phosphatase, dehydrogenase) were also noticeably higher, indicating a positive microbiome-host relationship. These studies highlight ZSBs' superior performance under aerobic rice, which is mostly attributable to improved nutrient diffusion, stable root zone pH and increased microbial respiration. Nonetheless, facultative anaerobic strain selection or formulation techniques such as biofilm-based inoculants may still be used to maximise performance in flooded rice.

Soil pH-dependent performance of zinc-solubilising bacteria in acidic and alkaline environments

Acidic vs. alkaline soils' ZSB response using the same strain: the pH of the soil has a significant impact on ZSB-mediated solubilisation mechanisms, particularly organic acid secretion and Zn complexation and is a key determinant of microbial survival and activity. *Pseudomonas chlororaphis* strain YB-10 was assessed in wheat and rice grown in both acidic (pH 5.2) and alkaline (pH 8.3) soils (26). Alkaline conditions inhibited acidification-mediated Zn release, as evidenced by the solubilisation index (SI), which was highest at neutral pH (6.8), followed by acidic soils (SI = 3.1) and lowest in alkaline soils (SI = 1.4). In acidic soils, the grain Zn content increased by 21.3 %, while in alkaline soils, it increased by 9.7 %.

Bacillus aryabhattai S-ZnB5 was investigated in rice grown in calcareous (alkaline), black (neutral) and red (acidic) soils (27). Zn availability rose by 33.4 % in acidic soils (pH 5.5) and grain yield increased by 16.2 % in tandem. However, only a 12.6 % increase in available Zn and a 5.3 % yield gain were noted in alkaline soils (pH 8.1). The limited solubility of ZnCO_3 and Zn(OH)_2 in high pH environments was cited as the reason for the decreased efficiency. *Burkholderia* sp. strains were tested in both neutral and acidic environments from Odisha (3). In alkaline environments, where Zn tends to precipitate and form stable complexes, the strain needed organic amendments (such as farmyard manure (FYM) or compost) to remain effective despite demonstrating good colonisation across pH ranges.

According to these results, ZSB strains have the best solubilising potential in acidic to neutral soils, whereas adaptable formulations (like organic carriers or chelators) or synergistic inoculants (like phosphate-solubilising bacteria (PSB)), which also secrete organic acids, are needed for performance in alkaline soils. ZSB-mediated Zn solubilisation is significantly influenced by soil pH, with acidic to neutral soils favouring microbial activity and Zn bioavailability.

Table 1. Zinc deficiency threshold in soil across different districts of Odisha

District	Deficiency	Soil Zn (ppm)	Reference
Balasore	Deficient	< 0.5 (Low)	(3)
Mayurbhanj	Deficient	0.3–0.7	(100)
Kendrapara	Deficient	< 0.5	(103)
Jajpur	Deficient	0.4	(100)
Bhadrak	Deficient	0.3–0.6	(101)
Balangir	Moderate deficiency	0.6–1.0	(102)
Nuapada	Moderate deficiency	0.7	(100)
Koraput	Slight deficiency	0.8–1.2	(100)

Zn deficiency threshold in soil is generally considered below 0.6 ppm for most crops.

Government initiatives for zinc nutrient management in rice-based systems

The Indian government has implemented many policies and programs to promote Zn supplementation, recognising that Zn deficiency adversely impacts food security. The National Mission on Sustainable Agriculture (NMSA) and the Soil Health Card Scheme are essential initiatives that advocate for balanced fertilisation by urging farmers to utilise Zn-enriched fertilisers in accordance with soil test recommendations (28, 29). These plans aim to rectify micronutrient deficits while enhancing soil fertility and crop productivity.

These programs have become more popular in Odisha, especially in districts where there is a lack of Zn. More and more people are recommending the use of Zn sulphate fertilisers for growing rice, which is the main crop in the area. Many research institutes from ICAR (Indian Council of Agricultural Research, India) and a few state universities of different states of India have done experimental trials that show that adding Zn to the soil or spraying it on the leaves can greatly increase the amount of rice produced and the amount of Zn in the grains (30–32). Also, researchers are looking into using Zn-enriched organic amendments and biofertilizers, like ZSB, as long-lasting and environmentally friendly alternatives to chemical fertilisers (Table 2).

Even with these improvements, small and marginal farmers still don't use Zn fertilisers as much as they should because they don't know enough about them, they can't afford them and quality inputs aren't always available in rural markets. To get more people to use Zn fertiliser, we need to improve extension services, farmer training programs and supply chain systems. Promoting bio-based interventions, such as microbial inoculants and Zn-enriched composts, is also a good way to improve Zn nutrition in a way that lasts, especially in places like Odisha where resources are limited (33).

Zinc-Solubilizing Bacteria as Plant Growth-Promoting Rhizobacteria (PGPR)

Plants require Zn as a micronutrient due to its significance in several biochemical and physiological activities, such as enzyme activation, protein synthesis and growth regulation. The Zn is prevalent in soils; yet, it frequently exists in forms that are inaccessible to plants,

resulting in significant Zn deficiency in agricultural systems. To address this issue, a particular group of beneficial soil bacteria known as ZSB has emerged as a viable biological agent for enhancing Zn availability in the rhizosphere. These bacteria are classified as Plant Growth-Promoting Rhizobacteria, recognised for their capacity to enhance nutrient uptake and facilitate diverse growth in plants (34).

Classification and isolation of zinc-solubilising bacteria

Zinc-solubilising bacteria are microbial strains that convert insoluble Zn compounds, including zinc oxide (ZnO) and Zn carbonate (ZnCO₃), into bioavailable forms for plants. The bacteria are derived from various taxonomic groups, primarily from the genera *Pseudomonas*, *Bacillus*, *Burkholderia* and *Rhizobium* (35–36). Isolation of ZSB from rhizospheric soil samples or plant roots is typically cultured on selective media that contain only insoluble Zn salts as the source of Zn. The presence of distinct halos surrounding colonies signifies the solubilisation of Zn. Quantitative estimation of Zn solubilization is often performed using spectrophotometric techniques to measure soluble Zn concentrations in culture filtrates (37–38).

Mechanisms of Zinc solubilisation by bacteria

ZSB can solubilise Zn through various biochemical mechanisms. A primary strategy involves the secretion of organic acids such as gluconic acid, citric acid and oxalic acid into the rhizosphere (Table 3). These organic acids create soluble complexes with Zn ions, facilitating the mobilisation of Zn from mineral sources (39, 40). *Pseudomonas aeruginosa* synthesis of gluconic acid significantly enhances Zn solubilisation (41). Bacterial cells release organic acids that decrease the environmental pH, facilitating the dissolution of Zn minerals (42). Siderophore synthesis, the secretion of iron-chelating chemicals by bacteria, has been associated with the transport of Zn. Siderophores primarily facilitate iron acquisition, although they also chelate other metal ions such as Zn, enhancing their solubility and uptake by plants (37). Alternative methods encompass the utilisation of oxidoreductive enzymes present on bacterial cell membranes and the synthesis of chelating ligands that bind to Zn ions. This multifaceted technique ensures effective Zn solubilisation despite variations in soil conditions.

Table 2. ZSB in enhancing zinc use efficiency and rice productivity across India

State	Soil type	Zinc solubilising bacteria strain(s)	Zinc use efficiency improvement	Rice productivity outcome	Reference
Odisha	Acidic, red lateritic	<i>Bacillus megaterium</i> CRS-30, CRS-17	↑ ZUE by ~30 % in red soils	↑ Yield by 18–25 %	(105)
West Bengal	Gangetic alluvial	Native <i>Pseudomonas</i> spp. + <i>Bacillus</i> spp.	↑ Zn uptake by 22 %	↑ Grain Zn content by 1.8–2.2 mg/kg	(106)
Punjab	Loamy, calcareous	<i>Bacillus subtilis</i> + organic formulation	↑ Zn efficiency in calcareous soil by 25 %	Yield increase of 12–15 %	(107)
Haryana	Sandy loam, neutral-alkaline	<i>Bacillus megaterium</i> , <i>Pseudomonas fluorescens</i>	↑ Zn solubilization in high pH soils	Better tillering; ↑ yield by 10–18 %	(108)
Chhattisgarh	Lateritic and clay loam	Local consortia (ZSB + PSB)	↑ Zn uptake in submerged soil by 28 %	↑ Yield by 20 % under SRI methods	(109)
Bihar	Alluvial, neutral	<i>Bacillus circulans</i> , <i>B. subtilis</i>	Improved Zn translocation efficiency	↑ Grain Zn by 1.6–2.0 mg/kg	(91)
Tamil Nadu	Clayey soils, pH 6.5–7.0	<i>Pseudomonas fluorescens</i> , encapsulated	↑ Zn bioavailability in irrigated paddy fields	↑ Yield by 12–16 %; improved root development	(110)
Andhra Pradesh	Deltaic soils	<i>Bacillus thuringiensis</i> , ZSB consortia	↑ Zn availability and root Zn transport	↑ Yield by 14 %, improved spikelet filling	(111)
Assam	Acidic and flood-prone	Indigenous ZSB strains from rhizosphere	↑ Zn use under waterlogged condition	↑ Panicle length, grain weight	(111)
Maharashtra	Medium black soils	<i>Bacillus subtilis</i> , <i>Azotobacter</i> with ZSB	Improved Zn-P synergy	↑ Yield by 10–12 % under semi-irrigated conditions	(112)

Note: ↑= Increased

Table 3. Mechanisms of zinc solubilisation

Pathway	Key agents	Factors
Organic acid production	Microbial species like <i>Pseudomonas</i> , <i>Bacillus</i> and <i>Aspergillus</i> spp. produce organic acids.	Microorganisms (e.g., bacteria and fungi) secrete organic acids (such as citric, oxalic, gluconic and tartaric acids) that chelate zinc ions and lower soil
Proton extrusion (acidification)	Microbial metabolism releases protons (H^+ ions) into the rhizosphere, decreasing pH and dissolving zinc compounds like zinc oxide or zinc carbonate.	Rhizosphere microorganisms and root cells actively release protons.
Siderophore production	Some microbes produce siderophores, high-affinity iron-chelating compounds that can also bind to zinc, facilitating its mobilisation and uptake.	<i>Pseudomonas</i> and <i>Azotobacter</i> species.
Enzymatic activity	Enzymes such as phosphatases can mineralise organic phosphorus compounds, indirectly enhancing zinc availability by altering soil chemistry.	Soil microbial enzymes in the rhizosphere.
Redox reactions	Microbial reduction or oxidation changes the chemical form of zinc, affecting its solubility and availability.	Soil microorganisms influencing redox potential.
Root exudation	Plant roots exude organic compounds (organic acids, amino acids) that solubilise zinc similarly to microbial acids.	Root exudates in the rhizosphere zone.

Bacterial genera involved in zinc solubilisation.

Various bacterial strains have demonstrated efficacy in Zn dissolution within laboratory and greenhouse settings. *Pseudomonas* species are the most extensively researched of them due to their exceptional ability to remove Zn (43). *Bacillus* spp., including *Bacillus thuringiensis*, have demonstrated significant potential in facilitating Zn mobility, hence enhancing Zn availability for crops (44). *Burkholderia cenocepacia* and *Rhizobium* species. Two other forms of ZSB enhance plant growth by increasing Zn availability (45). *Serratia marcescens* and *Serratia liquefaciens* are two significant strains that have efficient Zn-solubilising capabilities. These strains contribute to the catalogue of beneficial microorganisms applicable in sustainable agriculture (44).

Zinc-solubilising bacteria constitute a significant category of plant growth-promoting rhizobacteria (PGPR) that mitigate Zn deficiency in soils by converting insoluble Zn compounds into bioavailable forms for plant uptake. They accomplish this by synthesising organic acids, expelling protons, secreting siderophores and chelating. The inclusion of diverse taxa such as *Pseudomonas*, *Bacillus*, *Burkholderia* and *Rhizobium* in ZSB indicates their potential as bioinoculants to enhance Zn nutrition and agricultural yield sustainably. Subsequent investigations into the molecular mechanisms of Zn solubilisation and the application of these microorganisms in agricultural practices will enhance their utility in farming (46).

Agricultural and environmental significance of zinc-solubilising bacteria

Zinc-solubilising bacteria have gained considerable attention in sustainable agriculture due to their dual role in enhancing crop productivity and minimising environmental impact. By mobilising insoluble forms of Zn in the rhizosphere, ZSB can reduce dependence on synthetic Zn fertilisers, which are often costly and environmentally detrimental. The Zn deficiency is particularly widespread in calcareous and alkaline soils where native Zn availability is low (6). Beyond improving Zn uptake, ZSB have been shown to influence several physiological processes central to yield formation in crops like rice. Enhanced Zn availability through ZSB activity contributes to improved tillering, panicle initiation and grain filling by promoting key metabolic functions such as chlorophyll synthesis, auxin-mediated root development and enzymatic activation involved in carbohydrate metabolism and nitrogen assimilation.

These links remain underexplored. While improved Zn uptake is recognised, the effects of ZSB on photosynthesis, carbon allocation and source-sink dynamics during grain filling are poorly quantified. Claims of enhanced grain quality through Zn biofortification require validation using physiological indicators such as Zn remobilisation efficiency and transporter activity during reproductive stages. Recent findings suggest that ZSB bioinoculants not only enhance total yield but also improve grain Zn concentration, thereby contributing to nutritional security in Zn-deficient populations (35, 47). Furthermore, ZSB application promotes soil biological health, mitigating heavy metal accumulation and fostering a rhizosphere conducive to sustainable productivity (Fig. 3). A deeper understanding of these mechanistic pathways spanning rhizospheric Zn solubilisation to its physiological assimilation and grain deposition is crucial for integrating ZSB effectively into yield optimisation strategies (Table 4).

Impact of zinc-solubilising bacteria on plant growth and soil microbiome

Zinc-solubilising bacteria engage with plants and other soil microorganisms in dynamic manners, frequently establishing symbiotic or associative partnerships that facilitate nutrient uptake in plants. These bacteria inhabit the rhizosphere and root surfaces, where they excrete organic acids and siderophores that facilitate the proximity of Zn ions to the roots, enabling direct absorption by the plant (47, 48). The ZSB can coexist with beneficial microorganisms, such as nitrogen-fixing bacteria and phosphate solubilisers. Collectively, they can enhance plant growth. This assemblage of microorganisms facilitates nutrient mobility and enhances availability, rendering ZSB a crucial component of the rhizospheric microbial community (49).

Factors influencing the activity of zinc solubilising bacteria

Numerous environmental and physiological factors influence the efficacy of ZSB in dissolving Zn. Among these factors, soil pH plays a major role in regulating Zn solubility and microbial activity. Acidic soils often enhance the solubility of Zn, whereas alkaline soils impede its dissolution due to the formation of Zn compounds (50). ZSB modulate the quantity of organic acids produced and the protons released to enhance Zn availability (51). The presence of other metal ions, soil moisture, temperature and organic matter can alter bacterial activity and their efficacy in dissolving Zn. To utilise ZSB efficiently across various agroecosystems and to formulate optimal biofertilisers for each context, it is essential to understand these factors (13, 52).

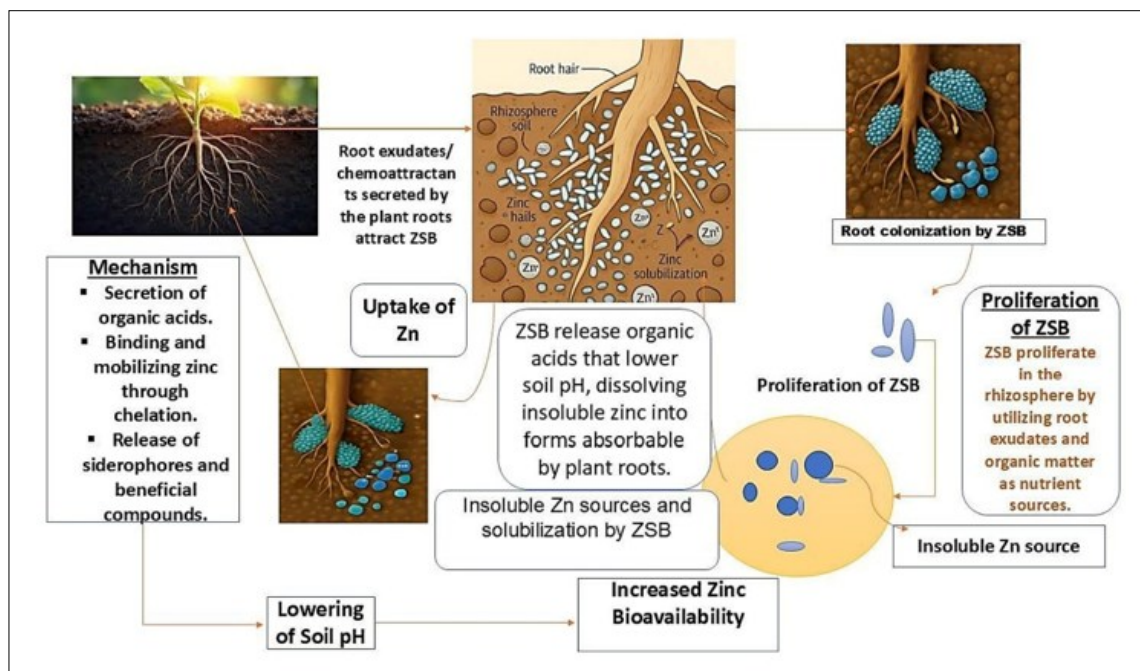


Fig. 3. Schematic representation mechanism of Zn solubilisation.

Table 4. Effect of application of Zn across different states of India

State/region	Soil type/condition	Zn application	Grain yield (kg/ha)	Grain Zn content (mg/kg)	Key findings
Odisha	Acidic sandy loam (pH 5.4)	ZnSO ₄ at 5 kg/ha soil + optional foliar spray at 0.1 %	~4937	~39.5	Soil Zn alone was as effective as the combined treatment; very high Zn accumulation.
Jharkhand (Ranchi)	Red lateritic (low OM, Zn deficient)	Zn at 2.5, 5.0, 7.5, 10 kg/ha	Up to ~2928	22.65–26.25	Best yield and grain Zn at 10 kg/ha ZnSO ₄ ; moderate Zn build-up at lower doses.
North-East (Nagaland, Meghalaya, Tripura)	Acidic/deficient soils	Soil Zn at 5 kg/ha; foliar at 0.5 %; Zn + ZSB combination	↑ yield (varied)	↑ Zn uptake	Foliar spray most effective; ZSB enhanced uptake and availability.
Punjab (Ludhiana)	Alluvial and low Zn	Soil Zn at 0–40 kg/ha	Optimal at 10–20 kg/ha	Improved grain/straw Zn	No additional gain beyond 20 kg/ha; Zn application enhanced nutritional value of Basmati rice.
Uttar Pradesh (Eastern districts)	Zn-deficient alluvial	ZnSO ₄ at 5–10 kg/ha	8–18 % increase	↑ Zn content	Zn application significantly improved yield in double-rice systems (rice-rice).
Karnataka (Southern zone)	Red sandy loam	ZnSO ₄ at 5 kg/ha basal; foliar spray 0.5 % at PI + flowering	~10–15 % increase	↑ grain Zn	Combined soil + foliar application best; synergistic effect observed.
Maharashtra (Konkan)	Lateritic soils	Soil Zn at 5–7.5 kg/ha	10–16 % increase	24–28	ZnSO ₄ effective in low-pH soils; zinc application corrected yield-limiting micronutrient deficiencies.
Tamil Nadu (Coimbatore)	Irrigated rice systems	Soil Zn at 5 kg/ha; foliar at 0.5 %	↑ by ~20 %	Up to ~30	Zn management enhanced tillering, panicle length and grain yield in high-yielding varieties.

Recent advancements in genomics and molecular biology have begun to elucidate the genetic mechanisms by which bacteria degrade Zn. Researchers have identified genes in certain ZSB strains that encode enzymes responsible for the production of organic acids, proton pumps and siderophores (53). This molecular information can enhance ZSB strains' ability to transport Zn and manage stress effectively. Furthermore, the integration of ZSB inoculation with contemporary agricultural practices such as precision farming and integrated nutrient management demonstrates potential for sustainable crop production (54).

Bioformulation strategies for zinc-solubilising bacteria

Zinc-solubilising bacteria have gained prominence as bioinoculants for ameliorating Zn shortage in crops, particularly in rice-based agricultural systems. The selection and formulation of microbial carriers are crucial for the effective distribution and performance of

ZSB in the field (55). Bioformulation technologies, ranging from conventional carrier-based systems to contemporary nano-encapsulation, are crucial for preserving microbial viability, ensuring precise delivery and enhancing stress resistance (56).

Comparison between carrier-based and liquid bioformulations

Carrier-based bioformulations are favoured due to their cost-effectiveness and ease of application. These systems often utilise solid substances such as peat, lignite, vermiculite and compost to retain and transport beneficial microorganisms. Peat and lignite have long been considered optimal selections due to their mechanical protection and ability to sustain microbial viability, maintaining colony-forming units (CFU) over 10⁷/g under adequate storage. However, these carriers frequently exhibit diminished performance in adverse field circumstances and have a shorter shelf life (57). Conversely, liquid bioformulations exhibit an extended shelf life and

enhanced stability during storage and application. They consist of stabilising substances such as glycerol, oils, or polyvinylpyrrolidone (PVP). They facilitate the uniform dissemination of microorganisms, enhance their thermal tolerance and increase their applicability, hence augmenting their utility in agriculture affected by climatic stress (58). Liquid formulations provide versatile application techniques such as seed coating, root dipping and fertigation, all of which ensure a uniform delivery of microorganisms (Table 5).

What constitutes an effective carrier for ZSB formulations?

An effective microbial carrier must be environmentally safe, cost-effective and non-toxic to humans. It must also sustain cellular viability for an extended duration. It should facilitate regulated release, protect bacteria from external challenges such as heat, UV radiation and desiccation and enable scalable processing (59). Promising solid transporters include peat and lignite, both of which harbour numerous bacteria that sustain life and continually safeguard the soil. Nonetheless, lignite by itself is not as efficacious as mixtures. Vermiculite and compost are biodegradable, durable and promote plant growth by retaining nutrients (Table 5). Alginate beads offer benefits for encapsulation, including accurate microbial release and enhanced field survivability (59). The particle size is crucial for their dispersion efficacy. Smaller particles adhere more effectively to surfaces and exhibit a higher likelihood of survival (60).

Methods for stabilisation, duration of efficacy and delivery mechanisms

The microbial strain and formulation matrix influence the stability and efficacy of ZSB bioformulations in delivering their contents. Peat and compost-lignite mixtures are examples of carriers that have demonstrated the ability to stabilise ZSB for several months (61). Advanced stabilisation techniques such as freeze-drying, the incorporation of trehalose and the selection of desiccation-resistant strains can significantly extend shelf life (61). For optimal outcomes in the rice rhizosphere, alginate bead encapsulation, vermiculite-based powder inoculants and liquid suspensions with protective additives are all effective alternatives. These approaches ensure uniform colonisation of the roots and maintain elevated microbial activity throughout the crop cycle (61). These approaches enhance ZSBs' resilience to abiotic stressors and improve its capacity to transport insoluble Zn.

Nano-bioformulation and microbial encapsulation

Recent advancements in nano-bioformulation technologies have enabled innovative methods for microbial delivery. These methods utilise nanomaterials such as silica, chitosan, or starch-based nanoparticles to safeguard the rhizosphere and facilitate the controlled release of bacteria (62). Nano-carriers facilitate the adhesion of Zn to root surfaces, enhance resistance to UV radiation and desiccation and promote absorption by plants. This renders them ideal for precision agriculture. Encapsulating ZSB in alginate beads or chitosan matrices enhances its viability throughout storage and transport, even under harsh pH or temperature conditions. The beads gradually release bacterial cells in the rhizosphere, hence prolonging the Zn solubilisation activity (63). Additionally, liquid nano-formulations that combine ZSB with stabilisers and nano-additives such as nano-silica create an inoculant that is user-friendly and manageable. Such formulations exhibit prolonged efficacy (6–12 months) and demonstrate superior plant colonisation, facilitating their utilisation by farmers across diverse agroecological zones (60, 64).

Field-validated ZSB strains and their capabilities

Multiple robust ZSB strains, including CRS-17, CRS-30, CRS-38 and CRS-9, have been identified and evaluated for field use. These strains are highly effective at degrading Zn-phosphate. These strains produce organic acids, particularly gluconic acid, which acidify the rhizosphere and facilitate the mobility of Zn (64). They enhance the solubility of indole-3-acetic acid (IAA), siderophores and other nutrients (such as phosphorus and potassium), hence promoting improved plant growth and nutrient absorption (57).

Zinc availability, uptake and metabolic functions in rice cultivation

Rice (*Oryza sativa*) serves as the primary sustenance for around half of the global populace, with Asia accounting for over 90 % of the world's rice production to satisfy the needs of its swiftly expanding population (65, 66). In Malaysia, adults consume about 2.5 servings of white rice daily, highlighting the crops' nutritional importance. To maintain and improve rice productivity, farmers frequently depend on chemical fertilisers that provide essential macronutrients N, P and K as well as micronutrients including Zn (Zn), boron (B), iron (Fe), copper (Cu), manganese (Mn) and molybdenum (Mo) (67, 68). The Zn is a vital

Table 5. Composition of different zinc solubilising bacteria bioformulations

Bioformulation Type	Microbial strains	Substrate material	Additives	Advantages
Carrier-based solid formulation	<i>Bacillus</i> spp. (e.g., <i>Bacillus subtilis</i> , <i>B. megaterium</i>), <i>Pseudomonas</i> spp., <i>Enterobacter</i> spp.	Peat, lignite, vermiculite, compost, talc, charcoal	Calcium carbonate, gypsum, sugar, biochar	Provides mechanical protection; supports microbial viability; cost-effective; commonly used in India; shelf-life 3–6 months
Liquid formulation	Same strains as above plus <i>Azotobacter</i> , <i>Azospirillum</i>	Mineral oil, water-based solutions, glycerol, emulsions	Surfactants, osmoprotectants (e.g., glycerol, PVP), nutrients	Longer shelf-life (~6–12 months); better consistency in delivery; easy handling and application as seed or soil inoculant
Alginate beads encapsulation	ZSB strains encapsulated in alginate matrix (e.g., <i>Bacillus</i> , <i>Pseudomonas</i>)	Sodium alginate + calcium chloride gel beads	Cryoprotectants (e.g., trehalose), nutrients	Controlled release; protection against environmental stresses (UV, desiccation); enhanced root colonisation; shelf-life up to 12 months
Nano-bioformulations	ZSB with nano-carriers like silica nanoparticles, starch nanoparticles	Nanomaterials combined with bio-carriers (alginate, glycerol-based liquids)	Stabilisers and slow-release polymers	Enhanced microbial stability and adhesion; improved zinc solubilization under stress; emerging technology with better field efficacy
Biochar-based Formulations	ZSB inoculated on biochar or charcoal powder	Biochar, charcoal	Nutrient amendments and moisture retainers	Improves soil structure and microbial habitat; synergistic benefits for nutrient cycling and carbon sequestration.
Powder formulations	Dried bacterial biomass (freeze-dried or spray-dried ZSB)	Talc, lignite powder, peat powder	Protective agents like skim milk powder, maltodextrin	Extended shelf-life; ease of transport and storage; requires rehydration before application
Granular formulations	ZSB immobilised on granules	Clay granules, expanded perlite, lignite granules	Nutrient additives, humic substances	Slow nutrient release; ease of soil incorporation; compatible with mechanised sowing

element necessary for several physiological and biochemical processes in plants that are crucial for growth and stress resilience (69, 70).

Zn availability and its impact on plant physiology

Zinc's bioavailability in soil is often limited because it forms insoluble complexes like ZnO, ZnCO₃ and zinc phosphate (Zn₃(PO₄)₂). This is especially true in calcareous or alkaline soils that are typical of flooded rice systems. Plants can't use these forms very well, which causes a Zn shortage that hurts important metabolic processes like glucose metabolism, protein synthesis, enzyme activation and hormone control (65). A lack of Zn slows down growth, lowers blooming and fruiting, lowers carbohydrate levels and makes it harder for plants to make phytohormones. This lowers crop yields and the nutritional quality of grains (71, 72). Zinc is an important cofactor for many enzymes, such as carbonic anhydrase, fructose-1,6-bisphosphate aldolase and alcohol dehydrogenase. These enzymes are important for photosynthesis, respiration and root growth (73). Zinc is important for keeping cell membranes intact because it stabilises phospholipids and protects them from oxidative damage through interactions with sulfhydryl groups (74, 75). Zinc changes the way hormones work, especially how auxin (IAA) is made and how abscisic acid (ABA) is changed. These hormones control growth, stomatal function and how plants respond to abiotic stress (70).

Increasing the availability of zinc through zinc-solubilising bacteria

Zinc fertilisers like zinc sulphate (ZnSO₄), zinc oxide and synthetic chelates like Zn-EDTA are common ways to deal with a lack of Zn (71). These fertilisers, on the other hand, often don't work well because Zn can build up in the soil, they cost a lot and they could harm the environment (68). The use of ZSB has become a viable biological option that naturally makes Zn more available to plants by changing insoluble Zn compounds into forms that plants can use (Table 6).

Pseudomonas, *Bacillus*, *Rhizobium*, *Actinobacter*, *Azotobacter* and *Enterobacter* are some of the species that use different methods to make Zn soluble. The main way this works is by releasing organic acids like gluconic acid, citric acid and oxalic acid, which make the rhizosphere more acidic and bind to Zn ions, making them easier to dissolve (13, 67). In addition, the production of siderophores, the release of protons and enzymatic redox processes all help to move Zn around (37). Bacterial activity makes it easier for roots to take up Zn, increases the number of different types of microbes in the soil and makes the soil more fertile overall (13).

Influence of zinc on plant development, yield and nutrient absorption

Inoculating plants with ZSB significantly improves their ability to absorb Zn, which is linked to more plant biomass, grain yield and nutrient intake. Studies in the field and greenhouse have shown that rice plants that have been treated with ZSB have longer and denser

roots, higher levels of chlorophyll and better resistance to abiotic stressors like drought and salt (42, 76). Zinc availability changes the way carbohydrates are distributed by turning on important enzymes in photosynthesis. This makes it easier for plants to get the energy they need to grow and reproduce (77-78).

Zinc works well with other minerals and PGPR, which helps crops grow better. When ZSB is co-inoculated with phosphate-solubilising bacteria or nitrogen-fixers, rice and other cereals absorb nutrients more effectively and produce more (13, 79). This synergy shows how useful microbial consortia could be in integrated nutrient management (INM) systems, where biological inoculants improve chemical fertilisers to make the most of nutrients and reduce their impact on the environment (68).

Integration of zinc solubilising bacteria with integrated nutrient management

ZSBs' incorporation into INM methods offers a sustainable way to improve crop productivity and alleviate the Zn shortage while lowering dependency on artificial inputs. INM emphasises the prudent use of biological, inorganic and organic inputs tailored to the unique requirements of crops and soil (76). Using native or imported microbial strains' Zn-solubilising properties helps farmers reduce their dependency on costly Zn fertilisers, enhance soil health and promote long-term agricultural sustainability (67). Studies emphasise the importance of site-specific management, whereby knowledge of microbial communities, environmental factors and soil Zn levels guides the effective use of ZSB-based biofertilisers (71, 72). To increase their use in rice production systems, resilient ZSB inoculants that are adapted to regional agroecological conditions must continue to be developed.

Recent developments in research on zinc-solubilising bacteria

According to recent research, ZSB play a critical role in increasing Zn bioavailability, particularly in the face of abiotic stressors like drought, salinity and heavy metal contamination, all of which are increasing in frequency as a result of intensive agriculture and climate change (80, 81). Research has demonstrated that inoculating rice plants under drought stress with ZSB strains, such as *Bacillus subtilis* and *Pseudomonas putida*, increased Zn solubilisation and antioxidant enzyme activities, which improved growth and yield. These results demonstrate ZSBs' many benefits, which go beyond nutrient mobilisation and include stress reduction and increased plant resilience (80).

The diversity and functional ability of native ZSB populations in rice rhizospheres across different agroecological zones have also been clarified by developments in metagenomics and high-throughput sequencing (82). These techniques have increased the possibility of developing region-specific bioinoculants by identifying new bacterial genera and species with potent Zn-solubilising properties and traits that promote plant growth. Microbial consortia have shown synergistic effects in improving Zn uptake and overall

Table 6. Comparison is based on typical results reported in agronomic research assessing zinc bioavailability and crop response

Treatment	Effect on yield (%)	Compared to control	Reason	References
Control	No Zn application or microbial inoculation	Baseline (0 %)	Natural soil zinc availability	
ZSB	Inoculation with zinc-solubilising bacteria	+ 10 % to + 25 % increase	Enhances zinc solubilisation and uptake; sustainable method (e.g., <i>Pseudomonas</i> , <i>Bacillus</i> spp.)	(45, 66)
ZnSO ₄	Application of zinc sulfate fertiliser	+ 15 % to + 35 % increase	Direct zinc supply; rapid correction of deficiency	(17, 104)

ZSB: zinc-solubilizing bacteria; ZnSO₄: zinc sulfate.

soil health when paired with organic amendments and precision fertilisation (13).

Molecular mechanisms and genetic engineering strategies

In the last few years, there have been big improvements in our understanding of the molecular processes that control how bacteria dissolve Zn. Genes that control glucose dehydrogenase, gluconic acid biosynthesis enzymes and siderophore synthesis pathways have been functionally characterised in several ZSB strains. This opens up the possibility of genetic improvement (83–84). Research indicates that increasing the amount of GCD in *Bacillus amyloliquefaciens* made more gluconic acid, which made Zn solubilisation work better in alkaline soil (83).

Researchers have used synthetic biology to change bacteria so that they can move Zn more easily and handle stress better. Research created a recombinant strain of *Pseudomonas fluorescens* that can dissolve both Zn and phosphate at the same time (84). This strain helps rice plants grow by making it easier for them to colonise. These new ideas could lead to the creation of biofertilizers that can do more than one thing and are tailored to the needs of specific crops and soils. This would improve sustainable nutrient management methods.

Integration of zinc solubilising bacteria with sustainable agricultural practices

The useful benefits of integrating ZSB inoculants into sustainable agricultural frameworks, like integrated nutrient management (INM) and organic farming systems, are highlighted by recent field trials. The ZSB combined with reduced amounts of chemical Zn fertilisers boosted rice yield by 15–20 % and increased grain Zn content compared to full-dose chemical fertilisation alone, according to research (59). In addition to lowering input costs, this also lessens soil erosion and environmental contamination. The ZSB has been shown to have synergistic effects on soil microbial diversity, disease resistance and nutrient absorption when applied in conjunction with other PGPR and mycorrhizal fungi. By recycling nutrients, reducing synthetic inputs and maintaining ecological balance, integrated bioinoculant consortia support circular agriculture.

Applications of zinc-solubilizing bacteria in global and Indian agriculture

ZSB bioformulations have demonstrated potential in a range of agroclimatic zones worldwide. In China, for instance, field application of *Pseudomonas* and *Bacillus* strains in calcareous and Zn-deficient soils resulted in improved plant hormone regulation, disease resistance and increased grain Zn concentrations in rice and maize (83). These strains help roots absorb Zn by producing siderophores, secreting gluconic acid and expressing Zn transport genes.

Trials on sugarcane and soybeans in Brazil showed that ZSB inoculants in conjunction with lower dosages of Zn fertilisers (ZnSO_4 or Zn-EDTA) preserved or even increased yields while drastically lowering the cost of chemical inputs. Through organic acid exudation, the bio-inoculants also increased the diversity of the rhizosphere microbiome and the availability of phosphorus, underscoring their multipurpose function in sustainable nutrient management (84).

Researchers have tested ZSB biofertilisers on staple crops like millet and maize in sandy, Zn-deficient soils in Africa, especially in sub-Saharan regions. The findings demonstrated notable gains in

drought tolerance, Zn bioavailability in edible portions and grain quality. Due to the regions' pervasive micronutrient malnutrition, this microbial approach is becoming more and more important in the fight against "hidden hunger" (59, 85). Additionally, in Bangladesh and Nepal, where Zn deficiency is common in rice paddies, integrated ZSB consortia have been assessed. Studies show that grain enrichment and Zn uptake can increase by up to 40 % without having a negative impact on soil biodiversity, indicating a great potential for low-cost biofortification substitutes in low-input farming systems (86).

Multiple pot and field experiments in India have demonstrated that ZSB particularly *Bacillus* spp., significantly enhance the yield of wheat and rice. Inoculation with robust ZSB strains led to significant enhancements in plant biomass, grain Zn concentration and overall yield in the eastern regions of West Bengal and Odisha (87). In Odisha, the state university studies at OUAT, strains such as BZ-2 and BZ-5 showed remarkable Zn and potassium solubilisation capabilities. Besides facilitating nutrient mobilisation and reducing the pH of the rhizosphere, these strains significantly enhanced plant development parameters such as dry matter accumulation, shoot and root length and seed germination (87, 88).

Farmer-led experiments at 339 on-farm sites in Odisha confirmed that applying ZSB and 50 kg ZnSO_4/ha in rice nurseries resulted in a 25 % increase in grain yield, as well as higher grain Zn concentrations and net economic returns (89). These results highlight the economic and agronomic viability of integrating ZSB in areas with low nutrient levels. Trials conducted on rice and wheat fields in Punjab and Chhattisgarh revealed comparable increases in organic carbon retention, microbial activity (particularly the enzyme dehydrogenase) and grain quality, suggesting long-term improvements in soil health (89). Furthermore, farmer participation in demonstrations was essential to the spread of technology. Following significant increases in crop vigour and productivity, farmers trained under integrated nutrient management programs swiftly embraced ZSB-based bio inputs. The ZSBs are an essential part of agroecological intensification in India because of the synergy seen in ZSB consortia (as opposed to single-strain use), which further improved nutrient cycling and crop resilience under both irrigated and rainfed systems (89).

A sustainable future for zinc-biofortification

The role of ZSB as natural biofortifiers is becoming more and more clear from South America to Odisha, as well as throughout Africa and East Asia. Especially in areas with acidic, red, or degraded soils, these microbes provide a comprehensive, economical and environmentally beneficial substitute for synthetic Zn fertilisers. Furthermore, they are essential to climate-resilient agriculture and sustainable soil management due to their favourable effects on rhizosphere health, nutrient cycling and farmer income (89). Scaling ZSB innovations now requires international cooperation, technology transfers from south to south and adaptive research using local strains. Their role extends beyond agronomy to include food security, environmental sustainability and the development of the bioeconomy, as evidenced by the growing alignment of ZSB bioformulation research with the Sustainable Development Goals of the UN (SDG 2: Zero Hunger; SDG 13: Climate Action) (90).

Challenges in field performance and translation from laboratory to field

Challenges in translating ZSB from laboratory screening to reliable

field performance arise from strong context-dependence of their activity and survival in heterogeneous soils. Under controlled in vitro conditions, ZSB are evaluated in optimised media, stable pH and low microbial competition, which rarely reflect field realities such as fluctuating moisture and temperature, spatially variable pH and redox conditions and diverse native microbiomes that compete for root exudates and niches. In alkaline or calcareous soils, rapid reprecipitation of solubilised Zn into ZnCO_3 or Zn(OH)_2 , combined with limited organic carbon, can markedly reduce the solubilisation observed in plates or pots, demanding co-application of organic amendments or consortia with other PGPR to maintain efficacy (89). Moreover, carrier quality, formulation stability and storage conditions often compromise the viability of ZSB inoculants by the time they reach farmers and inconsistent field practices in dose, placement and timing further contribute to variable yield and Zn-biofortification responses across sites and seasons. Therefore, robust bioformulations, multi-location and multi-season trials and integration of ZSB with complementary practices (balanced fertilisation, organic inputs and crop-specific consortia) are critical to narrow the gap between promising laboratory results and predictable on-farm outcomes.

Ecological and biosafety considerations

Ecological and biosafety considerations are critical when deploying ZSB as biofertilizers, because they are live, adaptable organisms introduced into complex soil ecosystems. The ZSB generally enhance Zn availability sustainably and can reduce dependence on chemical fertilisers, but they may also alter microbial communities, nutrient cycling and soil food webs in ways that are not fully predictable. Potential risks include unintended effects on non-target organisms, horizontal gene transfer with indigenous microbes and long-term shifts in soil microbial structure and function that persist even after the inoculant declines. Therefore, rigorous strain-level safety assessment (pathogenicity, antibiotic resistance), host- and site-specific testing and adherence to national biosafety and biofertilizer regulations are essential, along with multi-season monitoring of soil health indicators and microbial diversity under ZSB use (86).

Economic viability and adoption constraints for smallholder farmers

Economic viability and adoption of ZSB among smallholder farmers depend on whether the technology reliably increases yield and income while fitting within tight cash-flow and risk constraints. The ZSB-based inoculants can lower long-term fertiliser costs by partly substituting chemical Zn inputs and improving overall nutrient-use efficiency, but farmers often face higher upfront product prices, uncertain quality and variable field responses, which weaken their incentive to invest (84). Limited awareness of microbial technologies, weak last-mile distribution, lack of simple cost-benefit evidence (e.g., clear data on extra yield, net return and benefit-cost ratio per hectare) and restricted access to credit or extension support further slow adoption in smallholder systems. Building economic viability therefore requires affordable, stable ZSB formulations, integration with existing fertiliser practices (rather than full replacement) and demonstration plots or cluster trials that clearly show yield gains and net profit improvements under local conditions.

Constraints, Knowledge Gaps and Future Perspectives

The ongoing lack of certain micronutrients in agricultural soils,

particularly Zn (Zn), continues to be a major barrier to crop productivity and nutritional quality in India and other developing countries. Zn-deficient soils directly contribute to human malnutrition by impeding plant metabolic and enzymatic processes, resulting in suboptimal yields and decreased Zn bioavailability in consumable parts (90–92). In South Asia, where a substantial proportion of the population relies on staple crops with limited dietary diversity, the problem is particularly acute.

The extensive use of synthetic fertilisers and agrochemicals has worsened soil degradation and micronutrient imbalance. However, under field conditions, synthetic Zn fertilisers, such as Zn sulphate, can occasionally be ineffective or unaffordable, leading to a move towards sustainable alternatives. A sustainable method that could increase crop productivity and nutritional security is the use of ZSB, which increase the bioavailability of Zn in soils (45, 90–92). By releasing organic acids, producing siderophores and breaking down bound forms of Zn, these microbes act as organic biofortifiers in the rhizosphere.

Variability in field performance

Despite encouraging results in laboratory and greenhouse conditions, the field performance of ZSB remains inconsistent. These variable outcomes can be attributed to several interacting factors, including microbial strain specificity, soil physicochemical properties (e.g., pH, salinity, texture), crop genotype and agroclimatic conditions (93). For example, ZSB strains isolated from acidic or saline soils often fail to maintain viability or solubilisation efficiency in neutral or alkaline alluvial soils, suggesting a mismatch between microbial adaptation and target environments. Moreover, microbial competition with native soil microbiota and fluctuating abiotic stresses (e.g., temperature, moisture, or redox potential) can further compromise inoculant performance. This ecological incompatibility underscores the need for climate- and soil-specific strain selection, coupled with rigorous in situ validation before large-scale adoption.

Zn deficiency is severe in intensive cereal systems like the rice-wheat belts of eastern Odisha, Rajasthan and the Indo-Gangetic Plains due to nutrient depletion, leaching and low organic matter. Field trials by ICAR and state universities show that region-specific ZSB consortia with organic amendments can improve Zn uptake and yield (94). However, inconsistent results in alkaline or Zn-fixing soils highlight the need for a critical analysis of these variations and strategies to enhance ZSB performance.

Regulatory restrictions and defects in quality assurance

Microbial product regulations are still dispersed throughout the world. The majority of nations continue to rely on culture-based metrics, such as CFU counts, which are not representative of microbial viability in actual soil conditions. ZSB and other microbial biofertilizers are now subject to more stringent regulations in India as a result of recent changes made to the 2025 Fertiliser Control Order (FCO). Strain identity, minimum viable counts and efficacy data from multi-locational field trials must now be provided by manufacturers (95). Nonetheless, there are still issues with enforcement and compliance, particularly for small and mid-sized biofertiliser companies. Globally, agencies such as the United States Department of Agriculture (USDA) and the European Food Safety Authority (EFSA) are moving towards regulations that are function-oriented and strain-specific, utilising genomic tools to monitor inoculant strains after they have been applied. In order to facilitate

the international trade of biofertilisers, there is also growing demand for standardised international standards.

Climate-smart and strain-specific bioformulations

Multi-strain, multi-functional consortia that are suited to particular crops, soil types and climates are becoming more and more popular. These bioformulations are made to withstand a variety of abiotic stressors, such as drought, salinity and acidic pH, while simultaneously promoting plant growth, phosphate mobilisation and Zn solubilisation. The ZSB and other PGPR strains are being combined in climate-resilient microbial consortia experiments by startups such as Sea Energy in Bengaluru and Swadha Biotech in Gujarat. Similarly, IG Drones Bio (New Delhi) is leading the way in the drone-based deployment of microbial formulations, allowing for high-volume, consistent application over challenging terrain (96). This innovation is currently being tested in the maize belts of Chhattisgarh and the rice fields of Andhra Pradesh.

Combining AI and precision agriculture

ZSBs' integration with digital agriculture platforms is key to their future. Farmers can now apply bioinoculants according to site-specific requirements thanks to AI-driven analytics, soil health cards and remote sensing tools (97). Machine learning tools are being developed by companies such as Farmonaut and Boltzmann Labs to predict microbial efficacy based on weather forecasts, crop stages and historical field data. For example, when and where ZSBs should be applied, a combination of remote sensing (NDVI), soil sensors (pH, Zn status) and AI-driven advisory services can maximise impact and minimise resource waste (97). Under national programs like the Digital India Program and the National Mission on Sustainable Agriculture (NMSA), this data-driven, climate-smart approach is becoming more and more popular (96).

Worldwide patterns and cooperative frameworks

Outside of India, nations like China and Brazil are making significant investments in microbial inoculants for biofortification. Regional ZSBs for maize and soybeans are promoted by the Brazilian Agricultural Research Corporation (EMBRAPA). ZSBs are being used in low-input, nutrition-sensitive agriculture in Africa through cooperative programs with the International Institute of Tropical Agriculture (IITA). In the meantime, as part of its Green Deal policy, Europe's Horizon 2030 framework gives biologicals top priority for micronutrient enrichment.

Moving towards an agri-economy, i.e. biofortified and resilient

A vital connection between climate resilience, nutrition security and sustainable agriculture is Zn-solubilising bioinoculants. However, resolving the problems of technological integration, regulatory clarity and strain specificity is essential to their success (98, 99). If research, policy and field implementation work together, India, with its expanding bioeconomy and government-supported startup ecosystem, is well-positioned to spearhead this change. Bioinoculants are more than just soil amendments; they are strategic tools for creating a future that is environmentally sound and nutrient secure as we face mounting pressure to feed a growing population under climate stress.

Future prospects of zinc-solubilising bacteria in sustainable agriculture

Zinc-solubilising bacteria offer a transformative approach to Zn

biofortification, particularly in rice-based systems of developing countries like India. Future research should explore native ZSB diversity across agroecological zones and identify elite strains with superior Zn-solubilising and plant growth-promoting traits using advanced tools such as metagenomics, transcriptomics and genome editing. Integrating ZSB with other beneficial microbes (PSB, N-fixers, arbuscular mycorrhizal fungi (AMF)) can enhance nutrient use efficiency in Zn-deficient, acidic soils while reducing reliance on chemical fertilisers. Large-scale field trials and farmer-participatory studies are essential to validate their efficacy and adaptability. Incorporating ZSB technologies into national micronutrient and climate-smart agriculture programs, supported by policy incentives, can accelerate adoption, especially in tribal and low-input farming systems. Ultimately, ZSB-based bioformulations hold great promise for sustainable nutrient management, improved food security and environmental resilience.

Conclusion

Zinc malnutrition affects nearly one-third of the global population, particularly in cereal-based regions like India. Widespread Zn deficiency in red, lateritic and acidic soils such as those in Odisha reduces crop yield and grain nutrition. As inorganic fertilisation remains inefficient and unsustainable, ZSB emerge as eco-friendly alternatives. These microbes enhance Zn availability through organic acid and siderophore production, while also promoting growth via nitrogen fixation, phytohormone synthesis and pest suppression. ZSB use improves crop productivity and nutritional quality, reduces chemical fertiliser dependence and aligns with SDGs 2 (Zero Hunger), 13 (Climate Action) and 15 (Life on Land). Microbial biofortification thus offers a cost-effective, sustainable path to better soil health, nutrition and environmental resilience.

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Authors' contributions

AKM contributed to formal analysis, data curation and writing. SD and MMC contributed to formal analysis and data curation. CKS and MP contributed to formal analysis, investigation, review, writing original draft and review and editing, project administration and supervision. CP edited the manuscript. AM, ST and RKS contributed to formal analysis and editing the English language in the manuscript. SM reviewed the manuscript. All the authors read and approved the final manuscript.

Compliance with ethical standards

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References

- Morya R, Morya R, Mittoliya VK, Chhirouliya JK. Functions and deficiency symptoms of micronutrients. In: Desai NB, Sonkar A, Gupta D, Tiwari T, Suryabhan, editors. Novel approaches of nutrient management towards sustainability. Delhi: Integrated Publications; 2023. p. 35.
- Shukla AK, Behera SK, Prakash C, Tripathi A, Patra AK, Dwivedi BS, et al. Deficiency of phyto-available sulphur, zinc, boron, iron, copper and manganese in soils of India. *Sci Rep.* 2021;11(1):19760. <https://doi.org/10.1038/s41598-021-99040-2>
- Behera JK, Mishra P, Jena AK, Bhattacharya M, Behera B. Diverse agro-climatic zone impacts the soils' nutrient content and the fertility condition of Odishas' agricultural diversity. In: Adhikary PP, Shit PK, Laha J, editors. Soil, water pollution and mitigation strategies: a spatial approach. Cham: Springer Nature Switzerland; 2024. p. 315–38. https://doi.org/10.1007/978-3-031-63296-9_12
- Biswas S, Kundu DK, Mazumdar SP, Saha AR, Majumdar B, Ghorai AK, et al. Study on the activity and diversity of bacteria in a New Gangetic alluvial soil (Eutrocept) under rice-wheat-jute cropping system. *J Environ Biol.* 2018;39(3):379–86. <https://doi.org/10.22438/jeb/39/3/MRN-523>
- Dimkpa CO, Singh U, Bindraban PS, Adisa IO, Elmer WH, Gardea-Torresdey JL, et al. Addition-omission of zinc, copper and boron nano and bulk oxide particles demonstrate element- and size-specific response of soybean to micronutrients exposure. *Sci Total Environ.* 2019;665:606–16. <https://doi.org/10.1016/j.scitotenv.2019.02.142>
- Fasim F, Ahmed N, Parsons R, Gadd GM. Solubilization of zinc salts by a bacterium isolated from the air environment of a tannery. *FEMS Microbiol Lett.* 2002;213(1):1–6. <https://doi.org/10.1111/j.1574-6968.2002.tb11277.x>
- Salami A, Kene F. Zinc in plant membrane stability. *Biochem J.* 1970;119(3):609–13.
- Calvo P, Nelson L, Kloepper JW. Agricultural uses of plant biostimulants. *Plant Soil.* 2014;383(1):3–41. <https://doi.org/10.1007/s11104-014-2131-8>
- Noulas C, Tziouvalakas M, Karyotis T. Zinc in soils, water and food crops. *J Trace Elem Med Biol.* 2018;49:252–60. <https://doi.org/10.1016/j.jtemb.2018.02.009>
- Chowdhury FT, Zaman NR, Islam MR, Khan H. Anti-fungal secondary metabolites and hydrolytic enzymes from rhizospheric bacteria in crop protection: a review. *J Bangladesh Acad Sci.* 2020;44(2):69–84. <https://doi.org/10.3329/jbas.v44i2.51452>
- Singh R, Yadav M, Kumar V. Synergistic effects of microbial consortia including ZSB for sustainable rice cultivation. *Soil Biol Biochem.* 2023;174:108793.
- Bhattacharyya R, Ghosh BN, Mishra PK, Mandal B, Rao CS, Sarkar D, et al. Soil Degradation in India: Challenges and Potential Solutions. *Sustainability.* 2015;7(4):3528–70. <https://doi.org/10.3390/su7043528>
- Singh A, Sengar RS, Rajput VD, Minkina T, Singh RK. Zinc oxide nanoparticles improve salt tolerance in rice seedlings by improving physiological and biochemical indices. *Agriculture.* 2022;12(7):1014. <https://doi.org/10.3390/agriculture12071014>
- Khokhar JS, Broadley MR, and EL. Soil zinc surveillance frameworks can inform human nutrition studies: opportunities in India. *Front Soil Sci.* 2024;4:1421652. <https://doi.org/10.3389/fsoil.2024.1421652>
- Nayak AK, Pal D, Das S. Calcium pectinate-fenugreek seed mucilage mucoadhesive beads for controlled delivery of metformin HCl. *Carbohydr Polym.* 2013;96(1):349–57. <https://doi.org/10.1016/j.carbpol.2013.03.088>
- Adhikary S, Mandal N, Rakshit R, Das A, Kumar V, Kumari N, et al. Field evaluation of zincated nanoclay polymer composite (ZNCPC): impact on DTPA-extractable Zn, sequential Zn fractions and apparent Zn recovery under rice rhizosphere. *Soil Tillage Res.* 2020;201:104607. <https://doi.org/10.1016/j.still.2020.104607>
- Alloway BJ. Zinc in soils and crop nutrition. Paris: International Fertilizer Industry Association; 2008.
- Behera SK, Singh MV, Singh KN, Todwal S. Distribution variability of total and extractable zinc in cultivated acid soils of India and their relationship with some selected soil properties. *Geoderma.* 2011;162(3–4):242–50. <https://doi.org/10.1016/j.geoderma.2011.01.016>
- Prasad R, Shivay YS. Role of organic matter in micronutrient availability and crop nutrition. *Adv Agron.* 2021;168:143–80.
- Nishanth S, Shivay YS, Prasanna R. Enriching micronutrient status within soil systems and plants through microbial activity. In: Uphoff N, Thies J, editors. Biological approaches to regenerative soil systems. Boca Raton: CRC Press; 2023. p. 191–204. <https://doi.org/10.1201/9781003093718-21>
- Rattan RK, Patel KP, Manjaiah KM, Datta SP. Micronutrients in soil, plant, animal and human health. *J Indian Soc Soil Sci.* 2009;57(4):546–58.
- Gupta N, Ram H, Kumar B. Mechanism of zinc absorption in plants: uptake, transport, translocation and accumulation. *Rev Environ Sci Biotechnol.* 2016;15(1):89–109. <https://doi.org/10.1007/s11157-016-9390-1>
- Das AK, Lee DS, Woo YJ, Sultana S, Mahmud A, Yun BW. The impact of flooding on soil microbial communities and their functions: a review. *Stresses.* 2025;5(2):30. <https://doi.org/10.3390/stresses502030>
- Abu Bakar S, Jusoh N, Mohamed A, Muqoyyanah M, Othman MHD, Mamat MH, et al. Carbon nanotubes from waste cooking palm oil as adsorbent materials for the adsorption of heavy metal ions. *Environ Sci Pollut Res.* 2021;28(46):65171–87. <https://doi.org/10.1007/s11356-021-14918-y>
- Raj AB, Raj SK, Prathapan K, Radhakrishnan NV, Swadija OK. Effect of seed invigouration on yield enhancement in grain cowpea *Vigna unguiculata* (L.) Walp. *Legume Res.* 2021;44(9). <https://doi.org/10.18805/LR-4213>
- Xu W, Xu L, Deng X, Goodwin PH, Xia M, Zhang J, et al. Biological control of take-all and growth promotion in wheat by *Pseudomonas chlororaphis* YB-10. *Pathogens.* 2021;10(7):903. <https://doi.org/10.3390/pathogens10070903>
- Goswami B, Feuerstein TJ, Yadav R, Lebedkin S, Boden PJ, Steiger ST, et al. Thermally activated delayed fluorescence and phosphorescence quenching in iminophosphonamide copper and zinc complexes. *Chem Eur J.* 2021;27(61):15110–19. <https://doi.org/10.1002/chem.202101247>
- Ministry of Agriculture & Farmers Welfare. Annual report on fertilizer use and soil health programs. New Delhi: Government of India; 2023.
- Jordan-Meille L, Rubæk GH, Ehlert PAI, Genot V, Hofman G, Goulding K, et al. An overview of fertilizer-P recommendations in Europe: soil testing, calibration and fertilizer recommendations. *Soil Use Manag.* 2012;28(4):419–35. <https://doi.org/10.1111/j.1475-2743.2012.00453.x>
- Singh S, Singh A, Dey R, Mahatma M, Reddy K, Singh AK, et al. Insights into the physiological and molecular responses of plants to iron and zinc deficiency. *Plant Physiol Rep.* 2022;26(4):626–35. <https://doi.org/10.1007/s40502-021-00620-1>
- Mishra V, Shukla P, Shukla K, Varshney V, Singh J, Srivastava S. Strategies for increasing zinc uptake efficiency in plants. In: Srivastava S and Kaur H, editors. Zinc in soil-plant continuum. Singapore: Springer Nature Singapore; 2025. p. 139–61. https://doi.org/10.1007/978-981-96-4253-3_6
- Rehman HU, Aziz T, Farooq M, Wakeel A, Rengel Z. Zinc nutrition in rice production systems: a review. *Plant Soil.* 2012;361(1):203–26. <https://doi.org/10.1007/s11104-012-1346-9>

33. Patra SK, Sengupta S, Das SS, Mazumdar D. Assessment of the interaction of copper and zinc with cadmium to reduce its toxicity in heavy metal-contaminated river basin soils. *Discov Soil*. 2025;2(1):2. <https://doi.org/10.1007/s44378-025-00030-x>
34. Vejan P, Abdullah R, Khadiran T, Ismail S, Nasrulhaq Boyce A. Role of plant growth promoting rhizobacteria in agricultural sustainability: a review. *Molecules*. 2016;21(5):573. <https://doi.org/10.3390/molecules21050573>
35. Pawar A, Ismail S, Mundhe S, Patil VD. Solubilization of insoluble zinc compounds by different microbial isolates in vitro condition. *Int J Trop Agric*. 2015;33:865–9.
36. Patel M, Sharma N, Singh A. Zinc-solubilizing bacteria mitigate drought stress and improve antioxidant defense in rice. *J Plant Nutr Soil Sci*. 2022;185(4):457–68.
37. Saravanan VS, Kalaarasan P, Madhaiyan M, Thangaraju M. Solubilization of insoluble zinc compounds by *Gluconacetobacter diazotrophicus* and the detrimental action of zinc ion (Zn^{2+}) and zinc chelates on root knot nematode *Meloidogyne incognita*. *Lett Appl Microbiol*. 2007;44(3):235–41. <https://doi.org/10.1111/j.1472-765X.2006.02079.x>
38. Rosier A, Medeiros FH, Bais HP. Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. *Plant Soil*. 2018;428(1-2):35–55. <https://doi.org/10.1007/s11104-018-3679-5>
39. Chang AC. Mechanisms of zinc solubilization by microorganisms. *Soil Biol Biochem*. 2005;37(3):475–84.
40. Lazo DE, Dyer LG, Alorro RD. Silicate, phosphate and carbonate mineral dissolution behaviour in the presence of organic acids: a review. *Miner Eng*. 2016;100:115–23. <https://doi.org/10.1016/j.mineng.2016.10.013>
41. Nitu R, Rajinder K, Sukhminderjit K. Zinc solubilizing bacteria to augment soil fertility - a comprehensive review. *Int J Agric Sci Vet Med*. 2020;8(1):38–44.
42. Wakatsuki T. Mechanisms of metal solubilization by microorganisms. *Soil Sci Plant Nutr*. 1995;41(1):173–82.
43. Mehmood N, Saeed M, Zafarullah S, Hyder S, Rizvi ZF, Gondal AS, et al. Multifaceted impacts of plant-beneficial *Pseudomonas* spp. in managing various plant diseases and crop yield improvement. *ACS Omega*. 2023;8(25):22296–315. <https://doi.org/10.1021/acsomega.3c00870>
44. Abaid-Ullah M, Hassan MN, Jamil MJM, Brader G, Shah MKN, Sessitsch A, et al. Plant growth promoting rhizobacteria: an alternate way to improve yield and quality of wheat (*Triticum aestivum*). *Int J Agric Biol*. 2015;17(1):51–60.
45. Kamran S, Shahid I, Baig DN, Rizwan M, Malik KA, Mehnaz S. Contribution of zinc solubilizing bacteria in growth promotion and zinc content of wheat. *Front Microbiol*. 2017;8:2593. <https://doi.org/10.3389/fmicb.2017.02593>
46. Sethi G, Behera KK, Sayyed R, Adarsh V, Sipra BS, Singh L, et al. Enhancing soil health and crop productivity: the role of zinc-solubilizing bacteria in sustainable agriculture. *Plant Growth Regul*. 2025. <https://doi.org/10.1007/s10725-025-01294-7>
47. Kaluski DN, Ophir E, Amede T. Food security and nutrition - the Ethiopian case for action. *Public Health Nutr*. 2002;5(3):373–81. <https://doi.org/10.1079/PHN2001313>
48. Saravanan VS, Kumar MR, Sa TM. Microbial zinc solubilization and their role on plants. In: Maheshwari DK, editors. *Bacteria in agrobiology: Plant nutrient management*. Berlin: Springer; 2011. p. 47–63. https://doi.org/10.1007/978-3-642-21061-7_3
49. Chang YC, Choi D, Takamizawa K, Kikuchi S. Isolation of *Bacillus* sp. strains capable of decomposing alkali lignin and their application in combination with lactic acid bacteria for enhancing cellulase performance. *Bioresour Technol*. 2014;152:429–36. <https://doi.org/10.1016/j.biortech.2013.11.032>
50. Khoshru B, Mitra D, Mahakur B, Sarikhani MR, Mondal R, Verma D, et al. Role of soil rhizobacteria in utilization of an indispensable micronutrient zinc for plant growth promotion. *J Critical Rev*. 2020;21:4644–54.
51. Wakatsuki T. Metal oxidoreduction by microbial cells. *J Ind Microbiol*. 1995;14(2):169–77. <https://doi.org/10.1007/BF01569900>
52. Alloway BJ. Zinc in soils and crop nutrition. 2nd ed. Brussels: International Zinc Association; 2002.
53. Sehwat A, Sindhu SS. Zinc-solubilizing microorganisms: contributions in nutrient availability and implications for crop productivity in sustainable agriculture. In: Sayyed RZ, Ilyas N, editors. *Plant holobiome engineering for climate-smart agriculture*. Singapore: Springer Nature Singapore; 2024. p. 183–213. https://doi.org/10.1007/978-981-99-9388-8_11
54. Sindhu SS, Sharma R, Sindhu S, Phour M. Plant nutrient management through inoculation of zinc-solubilizing bacteria for sustainable agriculture. In: Giri B, Prasad R, Wu Q, Varma A, editors. *Biofertilizers for Sustainable Agriculture and Environment*. Cham: Springer; 2019. p. 173–201. https://doi.org/10.1007/978-3-030-18933-4_8
55. Purakayastha TJ, Bhaduri D, Kumar D, Yadav R, Trivedi A. Soil and plant nutrition. In: Ghosh PK, Das A, Saxena R, Banerjee K, Kar G, Vijay D, editor. *Trajectory of 75 years of Indian agriculture after independence*. Singapore: Springer Nature Singapore; 2023. p. 365–411. https://doi.org/10.1007/978-981-19-7997-2_15
56. Guha AA, Harish S, Sendhilvel V, Kannan M, Sasikala R. Revamping the encapsulation of microbes and their metabolites to nanoscale: a strategy to enhance crop biocontrol. *J Nanopart Res*. 2025;27(5):117. <https://doi.org/10.1007/s11051-025-06314-1>
57. Singh D, Prasanna R. Potential of microbes in the biofortification of Zn and Fe in dietary food grains: a review. *Agron Sustain Dev*. 2020;40(2):15. <https://doi.org/10.1007/s13593-020-00619-2>
58. Chandra G, Aggarwal A, Kumar M, Singh AK. Effect of zinc and vitamin E supplementation on hormones and blood biochemicals in peri-partum Sahiwal cows. *J Trace Elem Med Biol*. 2018;50:489–97. <https://doi.org/10.1016/j.jtemb.2018.02.015>
59. Rojas-Sánchez B, Guzmán-Guzmán P, Morales-Cedeño LR, Orozco-Mosqueda MDC, Saucedo-Martínez BC, Sánchez-Yáñez JM, et al. Bioencapsulation of microbial inoculants: mechanisms, formulation types and application techniques. *Appl Biosci*. 2022;1(2):198–220. <https://doi.org/10.3390/applbiosci1020013>
60. Singh D, Prasanna R. Potential of microbes in the biofortification of Zn and Fe in dietary food grains: a review. *Agron Sustain Dev*. 2020;40(2):15. <https://doi.org/10.1007/s13593-020-00619-2>
61. Rai S, Mago Y, Aggarwal G, Yadav A, Tewari S. Liquid bioformulation: a trending approach towards achieving sustainable agriculture. *Mol Biotechnol*. 2024;66(10):2725–50. <https://doi.org/10.1007/s12033-023-00901-0>
62. Garrido-Gómez L, Vegas-Díaz A, Fernández-García J, Alvarez M. Systematic optical potentials for reactions with cluster-structured nuclei. *Phys Rev C*. 2024;109(5):054608. <https://doi.org/10.1103/PhysRevC.109.054608>
63. Halim MA, Rahman MM, Megharaj M, Naidu R. Cadmium immobilization in the rhizosphere and plant cellular detoxification: role of plant-growth-promoting rhizobacteria as a sustainable solution. *J Agric Food Chem*. 2020;68(47):13497–529. <https://doi.org/10.1021/acs.jafc.0c04579>
64. Chaudhary V, Yadav JS, Dutta RK. A critical appraisal on some geotechnical properties of soil stabilised with nano-additives. *Environ Dev Sustain*. 2024;26(6):13831–94. <https://doi.org/10.1007/s10668-023-03277-y>
65. Gontia-Mishra I, Sapre S, Deshmukh R, Sikdar S, Tiwari S. Microbe-mediated drought tolerance in plants: current developments and future challenges. In: *Plant microbiomes for sustainable agriculture*. Cham: Springer; 2020. p. 351–79. https://doi.org/10.1007/978-3-030-38453-1_12

66. Hussain A, Ali S, Rizwan M, Rehman MZ, Javed MR, Imran M, et al. Zinc oxide nanoparticles alter the wheat physiological response and reduce the cadmium uptake by plants. *Environ Pollut*. 2018;242:1518–26. <https://doi.org/10.1016/j.envpol.2018.08.036>
67. Figueiredo MDVB, Seldin L, de Araujo FF, Mariano RDLR. Plant growth promoting rhizobacteria: fundamentals and applications. In: Maheshwari DK, editors. *Plant growth and health promoting bacteria*. Berlin: Springer; 2010. p. 21–43. https://doi.org/10.1007/978-3-642-13612-2_2
68. Kumawat N, Kumar R, Khandkar UR, Yadav RK, Saurabh K, Mishra JS, et al. Silicon (Si)- and zinc (Zn)-solubilizing microorganisms: role in sustainable agriculture. In: Giri B, Prasad R, Wu QS, Varma A, editor. *Biofertilizers for sustainable agriculture and environment*. Cham: Springer; 2019. p. 109–35. https://doi.org/10.1007/978-3-030-18933-4_6
69. Kushwaha P, Kashyap PL, Pandiyan K, Bhardwaj AK. Zinc-solubilizing microbes for sustainable crop production: current understanding, opportunities and challenges. In: Solanki MK, Kashyap PK, Kumari B, editors. *Phytobiomes: current insights and future vistas*. Singapore: Springer; 2020. p. 281–98. https://doi.org/10.1007/978-981-15-3151-4_11
70. Liu S, Zhang R, Mao J, Zhao Y, Cai Q, Guo Z. From room temperature to harsh temperature applications: fundamentals and perspectives on electrolytes in zinc metal batteries. *Sci Adv*. 2022;8(12):eabn5097. <https://doi.org/10.1126/sciadv.abn5097>
71. Hussain S, Khan AM, Rengel Z. Zinc-biofortified wheat accumulates more cadmium in grains than standard wheat when grown on cadmium-contaminated soil regardless of soil and foliar zinc application. *Sci Total Environ*. 2019;654:402–8. <https://doi.org/10.1016/j.scitotenv.2018.11.097>
72. Hou J, Gao X, Entz MH. Enhancing zinc and iron bioavailability through crop rotation and organic farming: insights from a long-term study. *Field Crops Res*. 2025;322:109710. <https://doi.org/10.1016/j.fcr.2024.109710>
73. Akay A. Role of zinc in plant metabolism. *Plant Physiol J*. 2011;45(2):123–9.
74. Suganya A, Saravanan A, Manivannan N. Role of zinc nutrition for increasing zinc availability, uptake, yield and quality of maize (*Zea mays* L.) grains: an overview. *Commun Soil Sci Plant Anal*. 2020;51(15):2001–21. <https://doi.org/10.1080/00103624.2020.1820030>
75. Marschner H. *Mineral nutrition of higher plants*. 2nd ed. London: Academic Press; 1995.
76. El Sabagh A, Islam MS, Hossain A, Iqbal MA, Mubeen M, Waleed M, et al. Phytohormones as growth regulators during abiotic stress tolerance in plants. *Front Agron*. 2022;4:765068. <https://doi.org/10.3389/fagro.2022.765068>
77. Marschner H, Cakmak I. High light intensity enhances chlorosis and necrosis in leaves of zinc, potassium and magnesium deficient bean (*Phaseolus vulgaris*) plants. *J Plant Physiol*. 1989;134(3):308–15. [https://doi.org/10.1016/S0176-1617\(89\)80248-2](https://doi.org/10.1016/S0176-1617(89)80248-2)
78. Mousavi SR. Zinc deficiency in plants: causes and management. *Int J Plant Prod*. 2011;5(4):303–20.
79. Singh S, Chhabra R, Sharma A, Bisht A. Harnessing the power of zinc-solubilizing bacteria: a catalyst for a sustainable agrosystem. *Bacteria*. 2024;3(1):15–29. <https://doi.org/10.3390/bacteria3010002>
80. Patel PS, Singh SK, Patra A, Jatav SS. Root dipping, foliar and soil application of zinc increase growth, yields and grain zinc in rice (*Oryza sativa* L.) grown in moderate zinc soil of inceptisol order. *Commun Soil Sci Plant Anal*. 2022;53(15):1917–29. <https://doi.org/10.1080/00103624.2022.2069800>
81. Sharma R, Mehta P, Verma S. Role of zinc-solubilizing bacteria in alleviating heavy metal stress in crops: a review. *Environ Pollut*. 2023;311:119964.
82. Kumar S, Gupta R, Singh P. Metagenomic insights into zinc-solubilizing bacterial diversity in rice rhizosphere across agroecological zones. *Microb Ecol*. 2023;85(3):567–79.
83. Zhao Q, Li H, Zhang L. Functional characterization of glucose dehydrogenase gene in *Bacillus amyloliquefaciens* for zinc solubilization. *J Microb Biotechnol*. 2021;14(11):4552–62.
84. Chen L, Wang J, Li Y. Engineering *Pseudomonas fluorescens* for enhanced zinc and phosphate solubilization to improve rice growth. *Appl Microbiol Biotechnol*. 2022;106(2):789–802. <https://doi.org/10.1007/s00253-020-11086-w>
85. Rani S, Kaur J, Dhillon S. Field evaluation of zinc-solubilizing bacteria for enhancing rice yield and grain zinc biofortification under integrated nutrient management. *Agron Sustain Dev*. 2024;43(1):15.
86. da Silva RC, Degryse F, Baird R, Ajiboye B, Stacey S, Peacock A, et al. Zinc in ammoniated phosphate fertilizers: solid-phase speciation, solubility and use of barrier coatings to enhance zinc availability. *Soil Sci Soc Am J*. 2024;88(6):2156–66. <https://doi.org/10.1002/saj2.20744>
87. Verma S, Chakdar H, Kumar M, Varma A, Saxena AK. Microorganisms as a sustainable alternative to traditional biofortification of iron and zinc: status and prospect to combat hidden hunger. *J Soil Sci Plant Nutr*. 2021;21(2):1700–17. <https://doi.org/10.1007/s42729-021-00473-5>
88. Baral K, Shivay YS, Prasanna R, Kumar D, Srinivasarao C, Mandi S, et al. Enhancing physiological metrics, yield, zinc bioavailability and economic viability of Basmati rice through nano zinc fertilization and summer green manuring in semi-arid South Asian ecosystem. *Front Plant Sci*. 2023;14:1283588. <https://doi.org/10.3389/fpls.2023.1283588>
89. Panda A, Panneerselvam P, Mishra BB. Plant-microbe interaction in improving zinc nutrition in rice: a review. *Int J Plant Soil Sci*. 2024;36(6):420–35. <https://doi.org/10.9734/ijpss/2024/v36i64644>
90. Pal S, Shankar T, Majumder S, Adhikary R, Pal S. Impact of agronomic zinc biofortification on yield attributes, yield and micronutrient uptake of rice (*Oryza sativa* L.) in Southern Odisha. *Int J Exp Res Rev*. 2024;40:90–103. <https://doi.org/10.52756/ijerr.2024.v40spl.007>
91. Upadhayay VK, Singh AV, Khan A, Sharma A. Contemplating the role of zinc-solubilizing bacteria in crop biofortification: an approach for sustainable bioeconomy. *Front Agron*. 2022;4:903321. <https://doi.org/10.3389/fagro.2022.903321>
92. Khan A, Singh AV, Gautam SS, Agarwal A, Punetha A, Upadhayay VK, et al. Microbial bioformulation: a microbial assisted biostimulating fertilization technique for sustainable agriculture. *Front Plant Sci*. 2023;14:1270039. <https://doi.org/10.3389/fpls.2023.1270039>
93. Upadhayay VK, Singh J, Khan A, Lohani S, Singh AV. An insight in decoding the multifarious and splendid role of microorganisms in crop biofortification. *Int J Curr Microbiol Appl Sci*. 2018;7(6):2407–18. <https://doi.org/10.20546/ijcmas.2018.706.286>
94. Hussain A, Ali S, Rizwan M, Rehman MZ, Hameed A, Hafeez F, et al. Role of zinc-lysine on growth and chromium uptake in rice plants under Cr stress. *J Plant Growth Regul*. 2018;37(4):1413–22. <https://doi.org/10.1007/s00344-018-9831-x>
95. Upadhayay VK, Singh J, Khan A, Lohani S, Singh AV. Mycorrhizal mediated micronutrients transportation in food based plants: a biofortification strategy. In: *Mycorrhizosphere and Pedogenesis*. Singapore: Springer; 2019. p. 1–24. https://doi.org/10.1007/978-981-13-6480-8_1
96. Riedell WE, Osborne SL, Pikul JL Jr. Soil attributes, soybean mineral nutrition and yield in diverse crop rotations under no-till conditions. *Agron J*. 2013;105(4):1231–6. <https://doi.org/10.2134/agronj2013.0037>
97. Tamreihao K, Devi AK, Langamba P, Singh HN, Singh TS, Rajiv C, et al. Growth kinetics, improved plant growth and alleviation of water stress in tomato by water stress tolerant bacteria. *Antonie Van Leeuwenhoek*. 2022;115(12):1437–53. <https://doi.org/10.1007/s10482-022-01789-7>
98. Ahmad S, Kaushik R, Ghatuary R, Kotiyal A, Jarial S, Kumar R.

- Utilizing IoT and AI for soil health monitoring and enhancement in sustainable agriculture. In: IoT and Advanced Intelligence Computation for Smart Agriculture. Boca Raton: CRC Press; 2025. p. 110–25. <https://doi.org/10.1201/9781003527664-7>
99. Sharma V, Sheerswal A, Bisht S. Rhizobacteria revolution: amplifying crop resilience and yield in a changing climate through plant growth promotion. J Basic Microbiol. 2025:e039. <https://doi.org/10.1002/jobm.70039>
 100. Soil Testing Laboratory, Government of Odisha. Annual report on micronutrient status of soils in Odisha. Bhubaneswar: Government of Odisha; 2022.
 101. Das S, Green A. Zinc in crops and human health. In: Biofortification of Food Crops. New Delhi: Springer India; 2016. p. 31–40. https://doi.org/10.1007/978-81-322-2716-8_3
 102. Bandyopadhyay S, Ray P, Padua S, Ramachandran S, Jena RK, Roy PD, et al. Priority zoning of available micronutrients in the soils of agro-ecological sub-regions of North-East India using geo-spatial techniques. Agric Res. 2018;7(2):200–14. <https://doi.org/10.1007/s40003-018-0327-5>
 103. Patra A, Singh SK, Jatav SS, Rekwar RK. Assessment of micronutrients fractionations and mobility in soils of eastern Uttar Pradesh. Indian J Agric Sci. 2021;91(6):880–4. <https://doi.org/10.56093/ijas.v91i6.114291>
 104. Yadav A, Babu S, Krishnan P, Kaur B, Bana RS, Chakraborty D, et al. Zinc oxide and ferric oxide nanoparticles combination increase plant growth, yield and quality of soybean under semiarid region. Chemosphere. 2024;352:141432. <https://doi.org/10.1016/j.chemosphere.2024.141432>
 105. Ghosh M, Vijayakumar V, Kurungot S. Dendrite growth suppression by Zn²⁺-integrated nafion ionomer membranes: beyond porous separators toward aqueous Zn/V₂O₅ batteries with extended cycle life. Energy Technol. 2019;7(9):1900442. <https://doi.org/10.1002/ente.201900442>
 106. Biswas JC, Haque MM, Khan FH, Islam MR, Dipti SS, Akter M, et al. Zinc fortification: effect of polishing on parboiled and unparboiled rice. Curr Plant Biol. 2018;16:22–6. <https://doi.org/10.1016/j.cpb.2018.11.002>
 107. Sharma DK, Shukla S, Sharma KK, Kumar V. A review on ZnO: fundamental properties and applications. Mater Today Proc. 2022;49:3028–35. <https://doi.org/10.1016/j.matpr.2020.10.238>
 108. Potdar SB, Praveen BVS, Sonawane SH. Sonochemical approach for synthesis of zinc oxide-poly methyl methacrylate hybrid nanoparticles and its application in corrosion inhibition. Ultrason Sonochem. 2020;68:105200. <https://doi.org/10.1016/j.ultsonch.2020.105200>
 109. Balasaheb WV, Uttam C. An intelligent optimized fractional order sliding mode controller for biological system. Multimed Tools Appl. 2024;83(31):75511–32. <https://doi.org/10.1007/s11042-024-18194-z>
 110. Krishnan Kutty SK, Skandasamy Natchimuthu PD, Ranjithkumar R, Djearamane S, Tey LH, Wong LS, et al. Field trial to correlate mineral solubilization activity of *Pseudomonas aeruginosa* and biochemical content of groundnut plants. Open Life Sci. 2025;20(1):20221008. <https://doi.org/10.1515/biol-2022-1008>
 111. Nath A. Effect of zinc fertilization and microbial inoculants on productivity of chickpea (*Cicer arietinum* L.) [dissertation]. New Delhi: ICAR-Indian Agricultural Research Institute; 2021.
 112. Khandekar MAP. Development of microbial consortium of efficient strains of zinc and iron solubilizing micro-organisms as a liquid bio-inoculant and its effect on maize [dissertation]. Rahuri: Mahatma Phule Krishi Vidyapeeth; 2018.

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