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Zinc solubilizing bacteria for sustainable biofortification: Mechanisms, rhizospheric interactions, and emerging biotechnological approaches

Vineet Gupta [1], Neitya Pathania [1], Jhanvi Rajput [1], Varinder Kaur [2] and Gagandeep Singh [1, *]

[1] Department.of Research and Development, FermEx Biotech Pvt. Ltd., Plot no. 306, Phase-IX, Industrial area, SAS Nagar Mohali, PB, India 160062.
[2] Genesis Institute of Dental Sciences & Research, Ferozepur - Moga Rd, Firozpur, PB, India,152004
ORCID ID: Gagandeep Singh; 0000-0002-3126-2818
Neitya Pathania; 0009-0009-9401-7623
Jhanvi Rajput; 0009-0007-9945-4799
Varinder Kaur; 0009-0002-3846-0531
Vineet Gupta; 0009-0007-9945-4799

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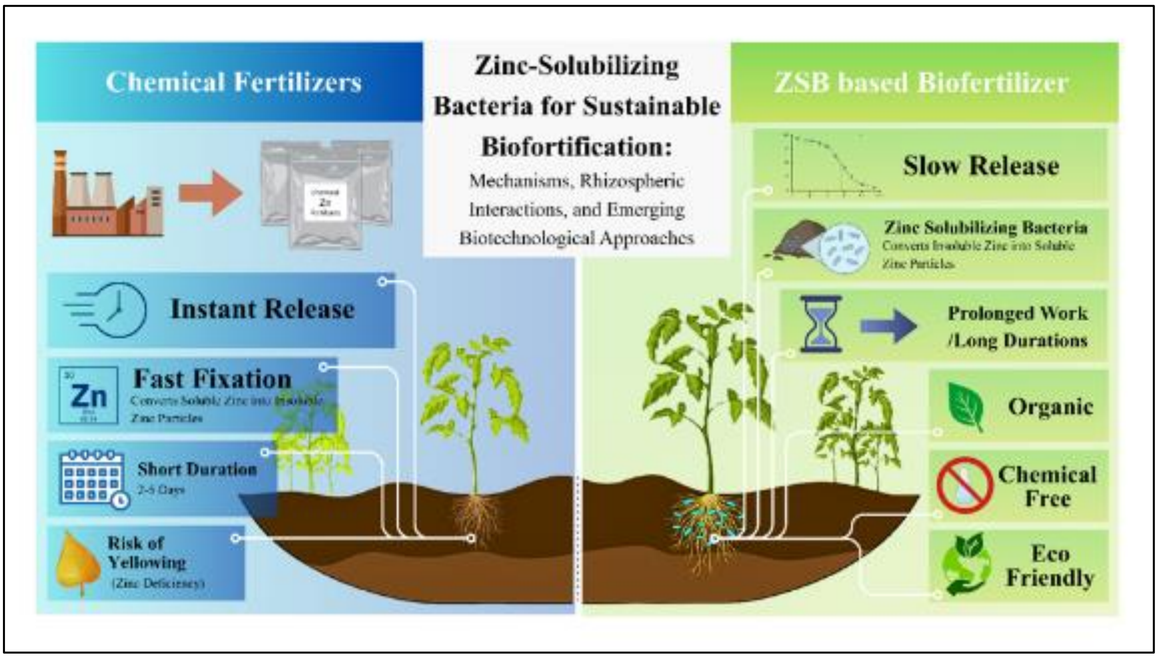
Abstract

Nutritional depletion of agricultural soils has resulted in widespread zinc (Zn^{2+}) deficiency or "hidden hunger," which is a major global public health challenge. Traditional agronomic and genetic bio fortification methods have sustainability and economic limitations, but microbial bio fortification using Zinc Solubilizing Bacteria (ZSB) offers an eco-friendly, sustainable option. This review discusses the mechanisms of ZSB for converting insoluble zinc complexes in soil to bioavailable Zn^{2+} through rhizosphere acidification by low-molecular-weight organic acids (LMWOAs), proton extrusion, siderophore chelation, and biofilm formation. We discuss the symbiotic dynamics of ZSB in the microbiome including partnerships with diazotrophs, phosphate solubilizers and mycorrhizae and the microbial regulation of the host plant ZIP transporters. The recent molecular advances are also reviewed such as the application of CRISPR-Cas9 genome editing targeting the glucose dehydrogenase (gcd) gene to re-route the metabolic flux toward hyper-solubilization, and the combination of ZSB with Nano biotechnology by means of bio-nanofertilizer. Despite field challenges related to rhizospheric persistence and formulation shelf-life, the inclusion of engineered climate resilient ZSB strains into sustainable agriculture represents a paradigm shift towards global nutritional security.

Keywords: Biofortification; Zinc Solubilizing Bacteria (ZSB); Hidden Hunger; Rhizosphere Acidification; CRISPR-Cas9; Bio-Nanofertilizers; Sustainable Agriculture

[*] Corresponding author: Gagandeep Singh

Graphical abstract



1. Introduction

The global recognition of the widespread micronutrient deficiency, or "hidden hunger", has been a major threat to human health and socio-economic development, as billions of people survive on staple crops that provide enough calories but are poor in nutrients (Das & Padhani, 2022). This structural nutritional deficit is predominantly a legacy of the Green Revolution that adopted intensive agricultural models to boost agronomic yields at the expense of crop nutritional density, and inadvertently triggered the systematic depletion of essential minerals from global soil profiles (Yilmaz & Yilmaz, 2025). The scarcity of bioavailable zinc (Zn) is one of the most severe of these deficiencies, resulting in impaired human immune function, stunting, and developmental delays (Bundela et al., 2025). Traditional interventions such as industrial food fortification or chemical fertilizer applications are often limited by high recurring production costs, environmental risks, and rapidly soil fixation chemicals (Prashar et al., 2025). Therefore, microbial bio fortification with Zinc Solubilizing Bacteria (ZSB) has become a very sustainable, environment friendly option (Gurubasajar & Basaiah, 2025). These specialized rhizospheric microorganisms secrete low molecular weight organic acids and siderophores actively to convert insoluble geological minerals into bioavailable Zn^{2+} ions (Upadhayay et al., 2022). By engineering the root microenvironment and the synergistic networks with host plants, ZSB can greatly improve the grain zinc loading and crop resilience (Sethi et al., 2025). The strategic integration of genome-edited "designer" strains and smart bio-nano fertilizers is an important milestone for modern precision agriculture and global food security (Hussain et al., 2026).

2. Concept of Biofortification

2.1. Biofortification

Biofortification is a sustainable agriculture approach which can be used to raise the amount and availability of nutrients in edible parts of the crop during the whole plant life cycle. It is applied primarily for solving the micronutrient deficiency or "hidden hunger" encountered by billions of people around the world (Rawal et al., 2024). Hidden hunger results when food intake is sufficient in calories but lacking in essential nutrients like zinc, iron, selenium and vitamin A (Das & Padhani, 2022). Staple foods such as rice, wheat, maize and legumes are an important component of the diet in the poor countries and improving their nutritional profile has been one of the major strategies in order to achieve food security and public health.

2.2. Need for Biofortification

Traditional farming systems stressed output over nutrition. The Green Revolution led to an enhancement of food production, however, the high-intensity farming has resulted in the depletion of soil micronutrients and has lowered nutritional density of crops (Yilmaz & Yilmaz, 2025). Consequently, soils and humans are increasingly suffering from deficiencies of micronutrients. Zinc and iron deficiencies have been linked to a weakened immune system, anaemia, poor growth and increased risk of disease. Thus, it is important to improve the nutrient density of staple crops to ensure nutritional security and human health (Bundela et al., 2025).

2.3. Advantages of Biofortification

Biofortification is different from industrial food fortification, which involves fortifying food after processing. It is a sustainable and long-term solution which is cost-effective and environmentally friendly. The nutrient-dense food from bio fortified crops is available forever without much modification of the diet or food distribution chain (Reddy et al., 2024). Moreover, bio fortification reduces nutritional supplementation and promotes sustainable farming practices.

2.4. Agronomic Biofortification

Agronomic bio fortification is the use of micronutrient fertilizers to the soil or plants to boost the uptake and retention of micronutrients. Zinc sulphate and zinc oxide are widely used fertilizers to biofortify the crop with zinc (Rawal et al., 2024). This practice can be beneficial for the availability of nutrients in short-term, however, in the long run, the soil's nutrient availability is often compromised by precipitation, adsorption and fixation processes (Prashar et al., 2025). Furthermore, application of fertilizers may cause increased production expenses and environmental problems.

2.5. Genetic Biofortification

The genetic biofortification is the process of using traditional breeding or genetic engineering to develop a crop variety that takes up, transports and stores more nutrients. The outcome is a number of various crops which are enriched with zinc in wheat and provitamin A in rice (Daveiga et al., 2020). The challenge with genetic biofortification is that it involves long term breeding efforts, sophisticated biotechnology techniques and extensive field trial testing.

2.6. Microbial Biofortification

Microbial biofortification is believed to be one of the most environment friendly and sustainable methods. This method utilizes beneficial soil micro-organisms to improve the solubility, mobilization and absorption of nutrients by plants (Gurubasajar & Basaiah, 2025). The rhizosphere is a region of nutrient cycling and several types of bacteria like zinc solubilizing Bacteria (ZSB), phosphate-solubilizing bacteria, nitrogen-fixing bacteria and mycorrhizal fungi play major roles (Gangadaran et al., 2025). These bacteria convert the nutrients from insoluble to soluble forms that a plant can absorb.

2.7. Role of zinc solubilizing bacteria

Zinc Solubilizing Bacteria are the most important microbes as it is able to break down the insoluble zinc compounds in soil into forms that plants can absorb. These bacteria have a positive effect on the uptake of zinc and nutritional value of crops (Saini et al., 2021). Other than solubilisation of zinc, ZSB also serves as a growth stimulator by secreting organic acids, phytohormones and other plant growth stimulating chemicals (Upadhayay et al., 2022). The environmentally friendly characteristics of ZSB and their ability to enhance the yields and nutritional value of crops are making them increasingly valuable in the fields of sustainable agriculture and nutritional security (Sethi et al., 2025).

3. Zinc Solubilizing Bacteria (ZSB)

Zinc Solubilizing Bacteria (ZSB) are useful rhizosphere bacteria which can convert insoluble zinc compounds to soluble zinc forms bioavailable to plants. In most soils for agriculture, zinc occurs in the bulk in the form of insoluble minerals like zinc oxide, zinc carbonate, zinc phosphate and zinc sulphide, particularly in alkaline and calcareous soils where zinc availability is low (Sukhwal et al., 2023). For this reason, ZSB are becoming a popular bioinoculants in sustainable agriculture, zinc biofortification and yield enhancement programs in the interest of environmental friendliness.

3.1. Mechanisms of Zinc Solubilisation

Zinc Solubilizing Bacteria (ZSB) convert the insoluble zinc compounds in soil into plant available zinc ions (Zn^{2+}) through acidification, chelation, proton release & alteration of rhizosphere (Upadhayay et al., 2022). These activities are coordinated, leading to more zinc being available in the rhizosphere and improving the uptake efficiency by the plants.

Table 1 Soil Zinc Transformations: Insoluble to Soluble Conversion Matrix on Different Crops.

Crop System	Native / Applied Insoluble Zinc Mineral Pool	Base Insoluble Form in Soil Matrix	Calculated Zinc Solubilisation Efficiency (SE %)	Reference
Rice *(Oryza sativa)*	locked in insoluble chemical complexes 96.0% - 99.0%	Zinc Oxide (ZnO) & Zinc Carbonate (ZnCO3)	109% to 244% active conversion based on colony halo-to-colony ratios.	Khanghahi etal., 2018
Wheat *(Triticum aestivum)*	The limitations of parent material and the interaction of high alkaline carbonate cause extensive soil fixation.	Zinc Carbonate $ZnCO_3$	214% – 244.9% (with elite strains such as Bacillus megaterium).	Yadav etal., 2023
Maize & Legumes *(Zea mays)*	Competing high phosphate fertilization blocks severe fixation lattices.	Zinc Phosphate Zn3(PO4)2	peak plate assay solubilisation indices of 530% - 631%.	Othman etal., 2022

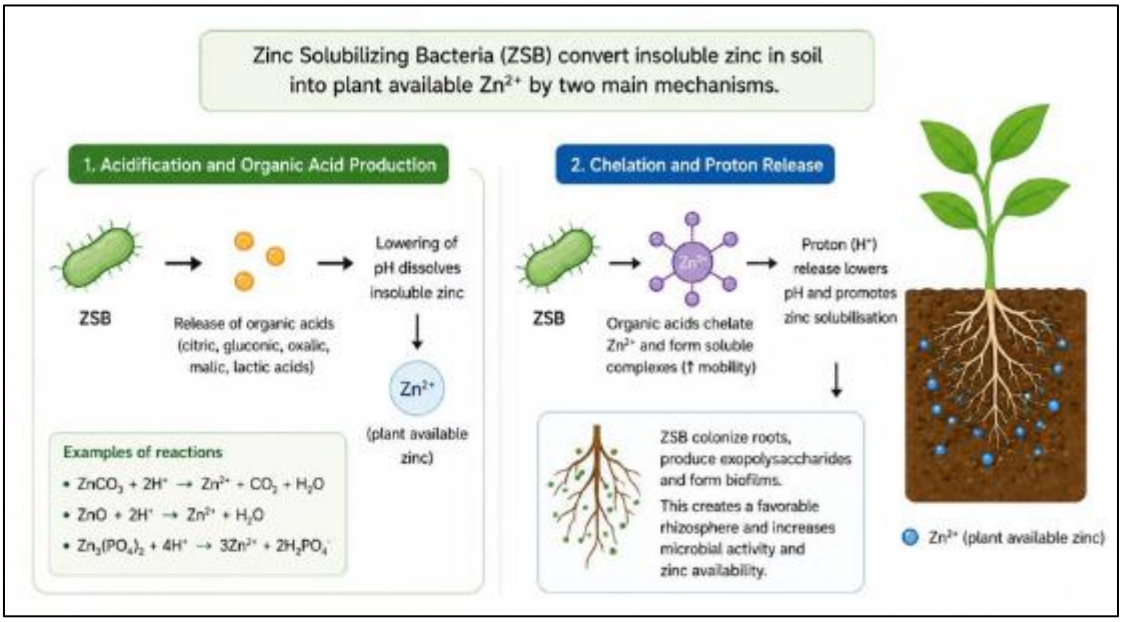


Figure 1 Mechanism to convert insoluble Zinc to soluble Zinc

3.1.1. Acidification and Organic Acid Production

The principal process is the release of low molecular weight organic acids such as gluconic, citric, oxalic, malic, and lactic acids, which lower rhizosphere pH and dissolve insoluble zinc minerals.

Zinc carbonate solubilisation occurs as:

$$ZnCO3 + 2H^{+} \rightarrow Zn^{2+} + CO2 + H2O$$

Similarly, zinc oxide is solubilized under acidic conditions:

$$ZnO + 2H^{+} \rightarrow Zn^{2+} + H_2O$$

And zinc phosphate dissolution proceeds as:

$$Zn_3(PO_4)_2 + 4H+ \rightarrow 3Zn2+ + 2H_2PO_4^{-}$$ (Kamalov et al., 2022)

3.1.2. Chelation and Proton Release

Organic acids also act as chelating agents forming soluble organic Zn complexes, which increase the mobility of zinc in soil. In addition, microbial metabolism causes proton extrusion, thus enabling zinc solubilization in the rhizosphere. ZSB form, colonize and coat the root surface with exopolysaccharides and form biofilms, thus creating a micro environment, small, stable and rich in nutrient which results in an increase in microbial activities (Naseem et al., 2022). These interactions help to facilitate movement of the plant root and microorganisms. These mechanisms present an alternative to the conversion of insoluble zinc forms to bioavailable Zn^{2+} to increase zinc uptake, plant nutrition and crop performance (Sethi et al., 2025). This makes ZSB a good zinc bio fortifier.

3.2. Plant Growth–Promoting Activities

Besides zinc-solubilisation, ZSB also have other plant growth promoting properties. They form growth substances such as indole acetic acid (IAA), gibberellins and cytokines, which promote the growth and absorption of the roots (Sukhwal et al., 2023). A few strains can also solubilize phosphate, mobilize potassium and fix nitrogen. Plants tolerance to abiotic stress, root surface colonization and soil aggregations are enhanced by ACC deaminase, siderophores, and exopolysaccharides (Geetakumari et al., 2025). The multifunctional properties of ZSB are very important as a stimulator of plant growth, enriching the soil with nutrients and fertility and as well as being important rhizosphere engineers.

3.3. Rhizospheric Interactions

Plant roots communicate with microorganisms in the physiologically active rhizosphere via root exudates, which contain sugars, amino acids, organic acids and signalling molecules. The exudates attract ZSB towards the surface of the roots where they will create an advantageous relationship with the plants called symbiosis (Lyu & Smith, 2022). Plants provide nutrients and good conditions for microbes while ZSB increases zinc bioavailability, nutrient cycling and root uptake of nutrients. In harsh environments development of biofilm and quorum sensing and microbial communication has been shown to be key to enhancing stress tolerance and uptake of zinc in recent studies (Tariq & Ahmed, 2023).

4. Synergistic Effects and Mechanism of Action

4.1. Mechanism Flow

The ZSB is a cohort of the rhizospheric microbiome that are responsible for enhancing the bioavailability of zinc via a complex biochemical progression. The process starts with secretion of gluconic, malic and citric acid also known as LMWOAs into the rhizosphere (Sethi et al., 2025). Upadhayay et al., 2022 reported, Insoluble zinc coordinates with tetrahedral and octahedral geometries to form crystalline lattice structures. These insoluble mineral lattice are further triggered by the LMWOAs in coordination with proton extrusion, results in Zn2+ ions release into the soil. Once converted, these ions are up taken by the roots via a specialized transport system, which further bridges the gap between plant metabolic system and soil minerals (Gupta et al., 2026).

4.2. Synergistic Interactions

4.2.1. ZSB & Phosphate Solubilizing Bacteria (PSB)

The symbiotic cycle of the ZSB and Phosphate Solubilizing Bacteria (PSB) helps create a strong nutrient solubilizing environment that utilizes organic acid production not only to increase the acidification but also to support the release of Zinc and Phosphorus into the rhizosphere (Upadhayay et al., 2025). Sethi et al., 2025, reported the synergy of these two types of bacteria not only ensure a balance nutrient profile of crop but also help prevent their common antagonistic behaviour of zinc uptake been prohibited by the high phosphorous levels.

4.2.2. ZSB & Mycorrhiza

The symbiotic relation of the ZSB and the Arbuscular Mycorrhizal Fungi (AMF) is of “Helper” and “Transporter” Respectively. The ZSB helps the AMF to colonize near the roots while AMF acts as a delivery system that delivers far off Zinc (Zn^{2+}) particle that are away from the root to ZSB and plant root (Yadav et al., 2023). This partnership significantly increases the plant’s total zinc acquisition capacity as well as expands the nutrient depletion zone.

4.2.3. ZSB & Nitrogen Fixers

ZSB directly boosts up the efficiency of nitrogen fixation cycle by providing zinc as it is a catalytic cofactor for the enzymes that play a vital role in the nitrogen fixation cycle. In leguminous plant especially this interaction of the ZSB and the nitrogen fixing bacteria like *Rhizobium* is quite essential (Gupta et al., 2026). In addition to this the amino acid precursors responsible for the synthesis of plant growth hormones as well as organic acids are provided by nitrogen fixing bacteria (Singh et al., 2024).

4.2.4. ZSB & Plant Growth Hormones (IAA, GA)

ZSB like *Bacillus spp.* and *Pseudomonas sp*. have the ability to synthesis phytohormones such as Gibberellins and Indole-3-Acetic Acid (IAA), that are responsible for promoting root elongation and lateral root development increasing the total surface nutrient absorption (Upadhayay et al., 2025). This leads to superior biomass and yield gain as the improved root architecture allows to greater zinc absorption and mobilization (Yadav et al., 2023).

4.3. Molecular Mechanism

4.3.1. sglcDH Gene (Gluconic Acid Production)

The glcDH gene is responsible for encoding the membrane bound enzyme called glucose dehydrogenase that largely governs efficacy of ZSB. The enzyme produced is capable of directly oxidizing glucose into gluconic acids within the periplasm (Upadhayay et al., 2022). The strategy of production of gluconic acid by the bacteria to reduce the pH and increase zinc solubilization is so far the best bacterial strategy (Sharma et al., 2012).

4.3.2. Siderophore Biosynthesis Genes

During the condition of Alkaline soil or deficiency of Fe or Zn, the ZSB activates a metabolic pathway that stimulates a certain gene cluster responsible for the synthesis and secretion of organic acid and sidrophores. They are small high affinity chelating compounds that form complexes with Zn^{2+} ions (Sethi et al., 2025). Through the mechanism of chelating the zinc ions, it is assured that the zinc particle does not get re-absorbed by the soil as well as does not form new insoluble compounds with it. Thus, maintaining its purity and solubility in an accessible form (Singh et al., 2024).

4.3.3. Zn Transporter Regulation

The ZIP gene family, consisting of the Zinc Regulated Transporters (ZRTs) and the Fe Regulated Transporters (IRTs) like protein are regulated by the microbial signals sent to regulate interaction between ZSB and host plant for zinc Solubilization (Gupta et al., 2026). To ensure the zinc ions are actively moving from the roots into the vascular system for the growth of plant leaves and grains, these genes are responsible for transport of zinc across membranes (Upadhayay et al., 2025).

5. Rhizosphere Region as a Hub of ZSB

5.1. Rhizosphere Microbiome Dynamics

Through continuous influx of energy-rich compound, the ZSB serves as ecological niches in the narrow zone of soil surrounding the plant root in the rhizosphere. By the actions of rhizodeposits deposition, the density of microbial presence can be seen of up to 10 to 100 time more than in bulk soil (Gupta et al., 2026).

5.1.1. Root Exudates as Carbon Source

About 40% of the photo synthetically fixed carbon in the rhizosphere is present in the form of exudates like sugars, amino acids and organic acids (Upadhayay et al., 2022). These exudates work as a primary sources of energy in ZSBs. Certain specific sugars like glucose works as a prerequisite for the metabolic pathway responsible for zinc solubilization, especially in species like *Pseudomonas* and *Bacillus* (Sharma et al., 2012). The main requirement of mineral dissolution is for the maintenance high metabolic rates and continuous production of gluconic acid by the ZSBs (Sethi et al., 2025).

5.1.2. Chemotaxis

Chemotaxis is the movement of bacterial cell towards the higher concentration of root- derived attractant like organic acids and phenolic compounds via specialized chemoreceptors that ZSBs have (Singh et al., 2024). A successful rhizosphere establishment and successive nutrient mobilization in *Enterobacter* and *Bacillus* isolates happens via chemotactic mobility which further outcompetes the non-beneficial microorganisms for nutrients and space (Krithika et al., 2016; Wu et al., 2025).

5.1.3. Biofilm Formation

Biofilms are the multicellular communities that have been organized from a planktonic state, once ZSB are attached to the roots. For a stable environment protected from stressors such as pH fluctuations and desiccation, the biofilms are protected in a matrix of self-produced extracellular polymeric substances (EPS) (Upadhayay et al., 2025). To avoid rapid diffusion of Zn^{2+} ions away from the roots and to maximize the efficiency of zinc solubilization, the biofilm ensures that the organic acid concentration stays put at the roots site by the ZSBs (Gupta et al., 2026).

5.2. Plant–Microbe Signaling

There is a highly regulated cross talk between the plant and their microbiome, while forming the ZSB population. It is not just a random functional establishment but a highly planned and defined one.

5.2.1. Flavonoids and Phenolic Compounds

The ZSBs beneficial for the plants detects the stress signals send by the plant to detect zinc deficiency via specific secondary metabolites secreted by the plants, known as the phenolic and flavonoids compounds. These compounds work like signaling molecules that can help attract and activate ZSBs as soon as they receive signals of being zinc deficient by the plant (Upadhayay et al., 2022). For the assurance of the plant's nutritional needs being met via a tailored microbial response, the ZSB upregulates the genes involved in root colonization and nutrient mobilization (Sethi et al., 2025).

5.2.2. Quorum Sensing (QS)

The ZSBs are capable of sensing their population density within the rhizosphere via specific molecules like N-acyl homoserine lactones (AHLs), they build a density dependent communication system to coordinate during collective behaviors. This particular phenomenon of ZSBs sensing their population via chemical communication is known as Quorum Sensing (QS) (Singh et al., 2024). Energy expensive processes that are capable of creating a physiological impact occur only in a bulk population, processes like expression of genes responsible for siderophore production, biofilm maturation and secretion of solubilizing enzymes, are all synchronized by high density population using QS (Gupta et al., 2026).

5.2.3. Root Colonization Factors

Structural factors for colonization like flagella, pili, and surface proteins are mediated by a number successful colonies, that allow ZSBs to firmly anchor onto the rhizoplane. The *Bacillus* species, in particular facilitates the adherence to root hairs via specific proteins like Biofilm Matrix Proteins, flagellar protein, and so on, that are primarily responsible for nutritional uptake (Wu et al., 2025). Most effective absorption of released Zn^{2+} molecules are precisely done by a molecular dialogue during colonization ensures by the ZSBs (Sharma et al., 2012).

5.3. Environmental Factors Affecting ZSB

The rate of microbial growth and stability of solubilized zinc is assured by, how sensitive the efficacy of ZSB is to the physiochemical environment of the soil. Soil pH plays the most important factor out of all the environmental factor that influences the zinc bioavailability as well as the functioning and performance of the ZSBs, for instance insoluble zinc are highly found in a calcareous soil or an alkaline soil (pH >7.5) in the forms of Zinc Hydroxide ($ZnOH^2$) or Zinc Carbonate ($ZnCo^3$) (Sethi et al., 2025). It is well known that ZSB thrives best in acidic conditions, however extreme pH conditions often inhibit bacterial growth and while sometimes denaturing the enzymes required for zinc solubilisation too (Upadhayay et al., 2025). By forming complex and stable metal-organic clusters, ZSB prevent the leaching out of soluble Zn from acidic soils (Singh et al., 2024).

5.3.1. Organic Matter

Larger microbial populations can be supported via additional carbon sources which can be provided by Soil Organic Matter (SOM), that acts both as a buffer for soluble zinc as well as a reservoir for ZSB (Gupta et al., 2026). Additionally, to keep zinc solubilized in a mobile state, bacterial siderophores work in a tandem with organic matters like Fulvic acid and Humic acids (Sethi et al., 2025).

5.3.2. Moisture and Oxygen

The microbial metabolic activities of ZSBs are highly dependent on how the solubilized nutrients are transported towards the root and is root exudates diffuse toward bacteria via the presence of adequate moisture and soil moisture potential (Yadav et al., 2023). ZSBs such as *Bacillus* and *Pseudomonas* are mostly aerobic in nature, excessive moisture can lead to anaerobic conditions that could shift the ZSB towards less efficient anaerobic mobilizers (Sharma et al., 2012).

5.3.3. Heavy Metals

Heavy Metals such as Cd, Pb, As, etc. can be competitive with zinc for the soil adsorption spots as well as bacterial binding sites. However, to fight this a few ZSB possess mechanisms such as intracellular sequestration or efflux pump that metal-resistant in nature allowing them to stay functional even in contaminated soils (Gupta et al., 2026). Immobilized toxic heavy metals are selectively left out and only zinc particles get absorbed by the ZSB through bio absorption (Singh et al., 2024).

6. Current Trends in ZSB Research

The research results on ZSB in the past few years have been mainly centered on multi-omics, integrated and application-based studies to boost uptake and production of zinc in plants. One of the major foci is the development of microbial consortiums having ZSBs co-cultured with phosphate solubilizing bacteria, nitrogen fixing bacteria, potassium mobilizers and arbuscular mycorrhizal fungi which will enhance nutrient cycling, rhizosphere function and plant growth promotion (Mohammed & Dakora, 2024). At the same time, formulations of nano-biofertilizer using ZSB and zinc nanoparticles are being investigated to improve the nutrient efficiency of delivery, control release and targeting the rhizosphere (Guardiola-Márquez et al., 2023).

A major achievement is the use of state-of-the-art omics technologies (metagenomics, transcriptomics, proteomics and metabolomics) to uncover the processes of zinc solubilisation, microbial communication and adaptation of rhizosphere microbial community. These techniques make it possible to identify functional genes that have a major influence on organic acids production, siderophore synthesis and resistance to stress, and thus, high efficiency microbial inoculants can be developed (Chukwuneme & Babalola, 2025). Furthermore, climate tolerant ZSB strains with the capability to thrive under abiotic stress such as drought, salinity, and temperature are coming to the fore, and are significant for climate-smart agriculture (Meena et al., 2025).

7. Role of Nano biotechnology in Zinc Biofortification and Solubilisation

The integration of nanotechnology with biological systems represents a paradigm shift in sustainable agriculture, especially for addressing the widespread soil Zn deficiency and human Zn malnutrition (Sethi et al., 2025). The conventional Zn fertilizers have low nutrient use efficiency because of rapid soil adsorption and fixation. On the other hand, the amalgamation of zinc oxide nanoparticles (ZnO-NPs) and zinc-solubilizing bacteria (ZSB) provides a new bio-nanofertilizer (B-NF) approach that facilitates the release of nutrients and targeted biofortification at the same time (Hussain et al., 2026; Mahmood et al., 2024).

7.1. Mechanisms of Nano-Zinc Solubilization

7.1.1. Nano-Zinc Solubilization Mechanisms

Compared to their bulk mineral analogues, ZnO-NPs are characterized by an extremely high specific surface area and surface reactivity which favors their translocation across biological barriers and their efficient distribution within plant vascular tissues (Jalal et al., 2023; Rani et al., 2022). Native ZSB species such as *Bacillus subtilis* and *Bacillus velezensis* act as biocatalysts in the rhizosphere and secrete organic acids, proton-chelating agents and siderophores which continuously solubilize the nano-scale ZnO. This process provides a continuous and demand responsive supply of bioavailable Zn (Mahmood et al., 2025; Shahid et al., 2025).

To reduce the nanoparticle toxicity and to retain the integrity of soil microbes, advanced B-NFs are designed by capping ZnO-NPs with microbial/microalgal extracts. These coatings modulate Zeta potential to a stable negative charge, which improves biocompatibility, seed germination and fertilizer stability (Guardiola-Márquez et al., 2023; Rani et al., 2022).

7.1.2. Crop Productivity and Biofortification

The co-application of ZnO-NPs and ZSB through seed priming or soil amendment optimized the seedling vigor indices by 32-46% and improved plant height, biomass accumulation and yield (Guardiola et al., 2023; Tondey et al., 2021). Agronomic bio fortification, by mixing soil application of ZnO-NPs together with ZSB and also doing low-dose foliar ZnO-NP sprays at the jointing or booting stages, can bump grain Zn concentrations in cereals something like 63.3–89.0% (Jalal et al., 2023 Mahmood et al., 2024). The foliar approach avoids soil immobilization, so there is stomatal uptake and a more direct Zn assimilation, which in turn improves photosynthetic carbon fixation. This is done via stimulation of Zn dependent enzymes such as carbonic anhydrase, (Sethi et al., 2025).

7.1.3. Nutrient Use Efficiency and Stress Resilience

Nano-zinc combined with plant growth-promoting bacteria tends to raise NUE as Zn can function like a natural urease inhibitor, yes even in a kind of urease way (Mahmood et al., 2025). When slow release ZnO-NPs are put on top of urea granules, and ZSB are inoculated at the same time, the timing match the nitrogen and zinc supply better. This synchronization helps with greater nitrogen recovery, a higher harvest index, and also more soil microbial biomass carbon (Mahmood et al., 2025; Hussain et al., 2026).

8. Role of Genetic Engineering

8.1. Phenotypic Bottlenecks and High-Throughput Genomic Mapping

Native zinc-solubilizing bacteria (ZSB) possess excellent basal metabolic profiles; however, their field agronomic performance is inconsistent due to competitive inhibition by native soil microbiomes and variable environmental stresses (Sethi et al., 2025). To overcome these phenotypic limitations, the transition from empirical bioprospecting to targeted genetic engineering is required to develop predictable bio inoculants with high performance (Sethi et al., 2025). The first step in high-throughput genomic profiling is 16S rRNA gene sequencing to obtain accurate taxonomic classifications and to identify elite wild-type template candidates (Rehman et al., 2023; Srithaworn et al., 2023). Metagenomic and whole genome sequencing allow researchers to systematically profile multi-gene clusters that drive target synthesis pathways and cellular mineral transporter functions (Sethi et al., 2025). One of the main targets of genome modification is the glucose dehydrogenase (gcd) gene that regulates the main direct metabolic pathway of glucose oxidation to mineral-solubilizing intermediates (Sethi et al., 2025).

8.2. CRISPR-Cas9 Locus Modification Architectures

Modern biotechnology leans on sequence specific class II CRISPR-Cas9 systems, to do pretty precise programmable changes at a given locus on the ZSB chromosome (Boti et al., 2023; Sethi et al., 2025). So, to tweak these metabolic frameworks, in this engineering workflow, the engineered single guide RNA, sgRNA complex somehow directs the Cas9 endonuclease to cut a defined double stranded break, DSB, at a chosen position inside the genome (Boti et al., 2023). After that, the host cell takes care of the damage, either it repairs it by error prone non homologous end joining, NHEJ, in order to generate disruptive insertion deletion, indel, mutations that knock out the target gen or it goes for high fidelity homologous direct repair (HDR) but only during an external donor DNA template is available, with flanking homology arms (Boti et al., 2023).

8.3. Metabolic Flux Redirection and Next-Generation Delivery Systems

Using CRISPR-Cas9 architectures, it could be possible to systematically knock out competing carbon-consuming metabolic pathways in order to deliberately redirect core cellular metabolic fluxes toward the overproduction of target solubilizing compounds (Boti et al., 2023; Sethi et al., 2025). At the same time, HDR enables the knock-in integration of potent, constitutive upstream promoters to drive continuous expression of mineral-mobilizing or siderophore-producing operons, effectively circumventing native microbial feedback inhibition mechanisms (Boti et al., 2023; Sethi et al., 2025). CRISPR mediated editing, can also drop in environmental stress-resilience cassettes straight into the bacterial chromosome, which lets engineered strains handle heavy-metal toxicity, salinity, and those temperature swings that show up in the field and these gene-edited bugs, are paired with placing engineered ZSB within biodegradable nano-biofertilizers, advanced polymer coatings, hydrogels, or even responsive biofilms, so the cells do not get knocked around by biotic and abiotic pressures, which helps with real world uptake. In this way, the formulation keeps a more stable, longer bacterial presence near the plant root zone, and improving nutrient assimilation across the whole crop lifecycle (Sethi et al., 2025).

9. Challenges and Limitations

The zinc biofortification potential and sustainable agriculture in the field of zinc are hampered by various biological, environmental and technological limitations of the Zinc Solubilizing Bacteria (ZSB) technique. Variability in soil properties, such as pH, moisture, texture, temperature and organic matter, can significantly influence microbial survival, colonization of rhizosphere, and efficiency of zinc solubilisation in the soil, at times leading to inconsistent performance of the soil in the field as compared to the lab (Upadhayay et al., 2022).

One of the most significant biological barriers is the lack of establishment in the rhizosphere, which leads to reduced persistence and functionality of introduced strains in the soil (Singh et al., 2025). In addition, abiotic stress factors like drought, salinity, temperature and nutritional imbalance under field conditions adversely affect microbial viability and efficiency (Soni et al., 2023). As far as technology, formulation instability is still a huge challenge, which brings about a shorter shelf life, loss of cell viability during storage, and inadequate carrier systems (Sarvepalli et al., 2025).

In addition, the gap between laboratory performance and in-field performance is still great, reducing the practical applications. Low awareness among farmers, less extension support and lacking defined quality control techniques are hindering the widespread adoption (Jha, 2023). The commercialization of ZSB-based technology will require powerful formulations, stress tolerant strains and consistent field validation to solve these issues.

10. Future Aspects

10.1. Development of Climate Resilient Multifunctional Strains

Research focuses on creation of multifunctional ZSB strains resistant to abiotic stresses such as drought, salinity, temperature and nutrient deficiency in the future (Upadhayay et al., 2024). Such inoculants prove crucial to guarantee performance in variable field conditions, including in the context of a changing climate.

10.2. Synthetic Biology and Genome-Assisted Improvement

In the future, genes responsible for organic acid production, proton expulsion and rhizosphere colonization can be targeted to be improved by means of advances in synthetic biology and genome editing. All these genome-assisted processes enables the construction of extremely effective “designer” ZSB strains (Guo et al., 2025).

10.3. AI enabled omics and microbial discovery

The use of AI-driven technologies will enable the identification of novel ZSB strains and pathways with omics technologies such as metagenomics, transcriptomic and metabolomics (Muhamed sharif, 2025). This also helps to predict microbial performance in various soil and climatic conditions.

10.4. Nano-biofertilizers and Advanced Delivery Systems

Nano-enabled biofertilizers and smart delivery systems are anticipated to enhance the survivability of the microbes, better control of the nutrients release and their stability in the field (Juthery et al., 2025). Shelf life and application efficiency might be improved by using encapsulation and carrier based technologies (Chand et al., 2025).

10.5. The integration of Precision and Regenerative Agriculture

ZSB integration with precision farming and regenerative farming might also improve nutrient use efficiency, decrease reliance on chemical fertilizers which has a few negative impacts on the environment, increase long-term improvement of soil health and ensure farming practices are climate-smart and sustainable (Sethi et al., 2025).

10.6. Global Environmental and Nutritional Security

In general, it can be assumed, that the zinc content of crops can significantly increase, the fertility of the soil mightimprove and in future climate scenarios sustainable agricultural systems can be possible, which will contribute to food security in the world in future using the ZSB technologies (Ali et al., 2023).

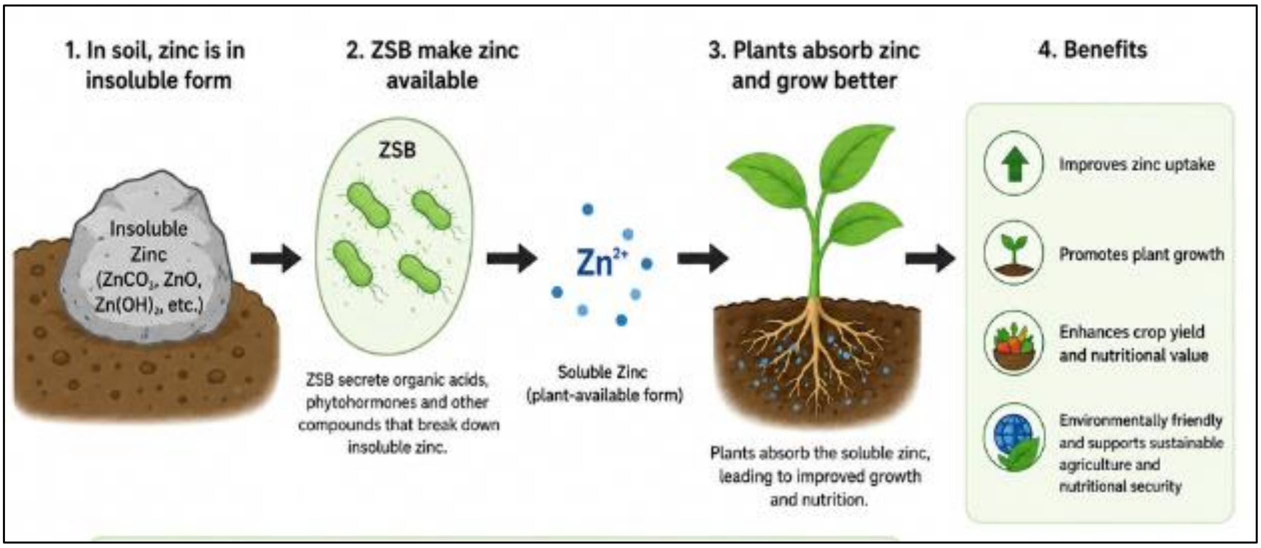


Figure 2 Mechanism and action of Zinc solubilisation by ZSB to Plants

11. Conclusion

Microbial biofortification, aided by Zinc Solubilizing Bacteria (ZSB), is a big step to tackle global hidden hunger and the slow loss of soil nutrients, without really putting the environment at risk (Gurubasajar and Basaiah, 2025). In a practical sense, ZSB manages to free up the chemical "stock" of insoluble soil zinc using a few core biochemical routes: like rhizosphere acidification driven by low-molecular-weight organic acids, siderophore mediated binding (chelation) and then the steady building of a biofilm like matrix, so in the end the zinc gets shifted into plant-available Zn^{2+} (Upadhayay et al., 2022).

On top of that, their functional cooperation with other soil microbes, plus the direct boosting of the host plant ZIP transporter genes, strongly helps raise micronutrient build-up inside edible grains (Gupta et al., 2026; Sethi et al., 2025). Still, once you move to actual fields, a few obstacles show up, such as uneven rhizospheric colonization, issues with product formulation staying stable, and shifting environmental pressures (Sarvepalli et al., 2025). These things delay broad commercial use, even though newer molecular tools are starting to look like a way forward.

So the direction now leans toward more advanced synthetic biology designs, for example CRISPR-Cas9 genome editing aimed at the gcd metabolic pathway, and also the encapsulation of these microbes into targeted bio-Nano fertilizers. With that, the strains are better equipped with a kind of "precision" plus climate tolerance, which makes open-field agronomy more realistic (Boti et al., 2023; Hussain et al., 2026). If engineered biological systems like these are actually rolled into mainstream precision agriculture and regenerative farming, then over time we can expect a scalable, lower-cost paradigm shift, which matters a lot for long-term global nutritional security, and for keeping sustainable food chains running (Sethi et al., 2025).

Compliance with ethical standards

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Disclosure of conflict of interest

The authors declare that there is no conflict of interest.

Authors Contribution

VG provided the concept, NP and JR drafted the article, VK Prepared Graphics, GS critically reviewed article and revised. All authors approved the final draft of article for the publication.

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