



# Cross Talk Between Zinc-Solubilizing Bacteria and Plants: A Short Tale of Bacterial-Assisted Zinc Biofortification

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A contemporary approach to bacterially mediated zinc (Zn) biofortification offers a new dimension in the crop improvement program with better Zn uptake in plants to curb Zn malnutrition. The implication of Zn solubilizing bacteria (ZSB) represents an inexpensive and optional strategy for Zn biofortification, with an ultimate green solution to enlivening sustainable agriculture. ZSB dwelling in the rhizospheric hub or internal plant tissues shows their competence to solubilize Zn *via* a variety of strategies. The admirable method is the deposition of organic acids (OAs), which acidify the surrounding soil environment. The secretion of siderophores as a metal chelating molecule, chelating ligands, and the manifestation of an oxidative–reductive system on the bacterial cell membrane are further tactics of bacterially mediated Zn solubilization. The inoculation of plants with ZSB is probably a more effective tactic for enhanced Zn translocation in various comestible plant parts. ZSB with plant growth-enhancing properties can be used as bioelicitors for sustainable plant growth *via* the different approaches that are crucial for plant health and its productivity. This article provides an overview of the functional properties of ZSB-mediated Zn localization in the edible portions of food crops and provides an impetus to explore such plant probiotics as natural biofortification agents.

**Keywords:** biofortification, zinc solubilizing bacteria, zinc, zinc malnutrition, plant growth

## INTRODUCTION

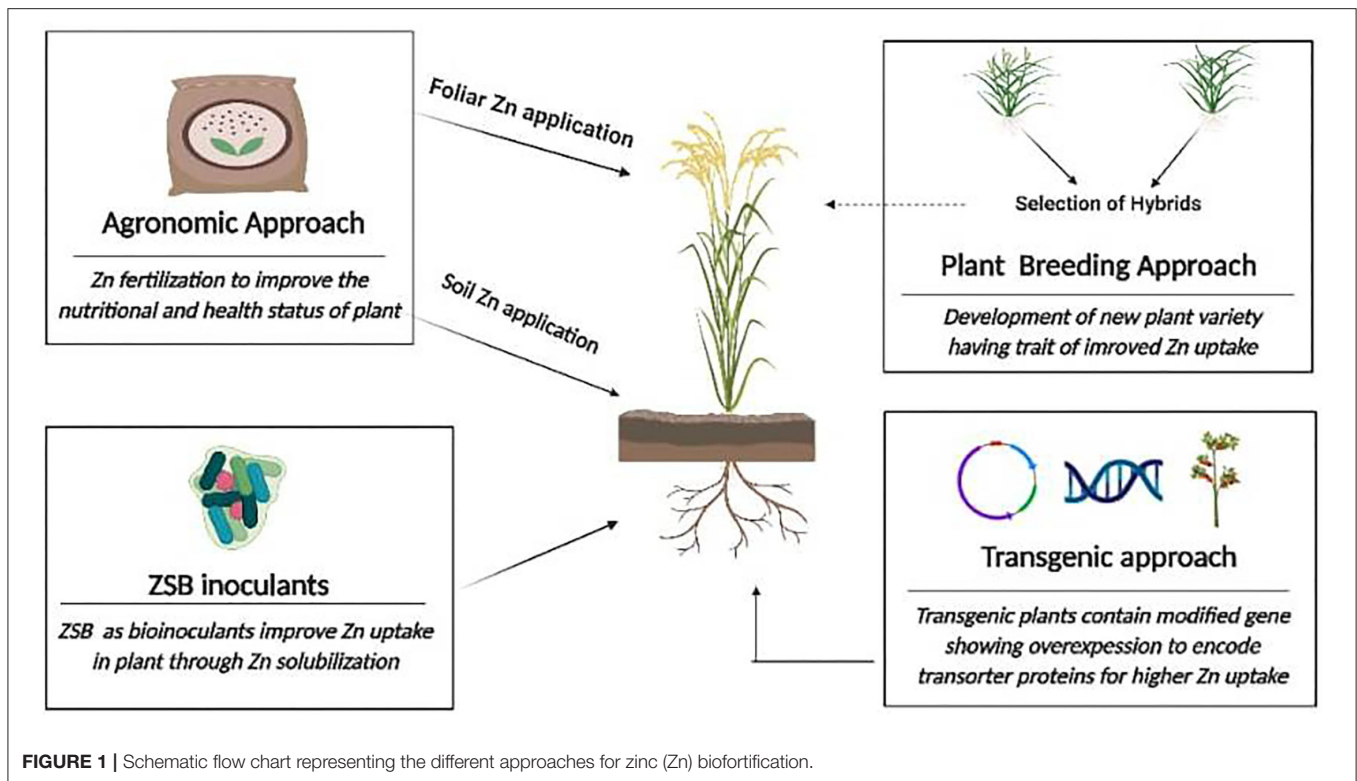
Recently, zinc-solubilizing bacteria (ZSB) have been updated with the addition of a biofortification approach called microbial-assisted crop biofortification. The benevolent job of microbes in the ecological nutrient cycle has been deliberated for many decades. The current understanding of ZSB and their use in biofortification had been elucidated up to some extent impalpably. Even fewer studies on an interplay between plants and ZSB and their exploration for improved plant growth in applied settings gave the hope of solving the problem of zinc (Zn) malnutrition in a sustainable way. Zn is considered to be a vital micronutrient for cellular life, but Zn deficiency leads to a wide variety of metabolic disorders, which in humans manifests itself in a wide variety of diseases (1). The production of crops with Zn enriched edible portions (fruits, seeds, etc.) for poor people who are relying on food-based crops as diet with an inadequate amount of Zn (less than the daily required amount) is the current footstep to conquer the micronutrient deficiency, which is also supported

by WHO in the wellbeing of huge section of deprived people (2, 3). In agronomical practices, biofortification approaches through agronomic, plant breeding, and biotechnological intrusions are mostly used to achieve an improved uptake of Zn and other micronutrients in the eatable plant parts (4–7). The productive function of ZSB on crop overall development and health has already been described in the literature, while, in contrast, ZSB have been selected as natural biofortification agents to amplify the Zn concentration by being part of either the rhizomicrobiome or the phytomicrobiome. A few authors have proposed microbial-assisted biofortification and, in particular, discussed ZSB as “rhizobacteria” or “endophytes” if ZSB were isolated either from the soil sample(s) of rhizospheric origin or from the inner plant tissue. The precise effect of Zn mobilization that ZSB brings about is the deposition of organic acids (OAs), which acidify the surrounding soil environment and solubilize Zn due to the drop in pH (8, 9). Other mechanisms include the secretion of chelating agents, like siderophores, which are believed to play a critical role in iron (Fe), Zn, and the solubilization of other micronutrients (10). ZSB secrete some organic compounds related to plant growth, namely phytohormones and siderophores, thus supporting the growth of cultivated plants (11). ZSB-mediated plant growth results from the effect of either “direct” or “indirect” plant growth-related mechanisms shown by ZSB inoculants. In the direct mechanisms, ZSB support the acquirement of essential micronutrients through the deposition of OAs and enzymes and can change the phytohormone level in the plant. The nutrient absorption facilitated by ZSB can classically include Zn, Fe, phosphorus, potassium, and nitrogen. The indirect mechanism profile includes the synthesis of secondary metabolites, in particular, antifungal and antibacterial compounds that can reduce the damage to plants from infection with phytopathogens (such as soil fungi and bacteria). As an effectual bioelicitor, ZSB maintained a proper decorum of better plant probiotics by increasing plant growth-attributed characters such as plant length and dry biomass. Their role in the enhancement of crop yield has made them a prolific contributor to better plant bioinoculants, while soil fertility restoration after ZSB inoculation has yet to be studied in depth. ZSB, which have many plant growth elevating features, dissolve Zn in the soil and facilitate its translocation from the soil settings into various tissues of plants (12). The Zn enrichment in grains shows the power of ZSB to make plants nutritionally rich to counteract Zn malnutrition. This aspect is more economically feasible than other aspects of biofortification including agronomic and biotechnological bases and can maintain agricultural production without adapting the chemical fertilization strategy (13). This enables the environment friendly approach of microbial-based fertilization to maintain the overall plant health and ascertains the “green technological” approach to biofortification (14). However, some reports currently highlight the job of ZSB in plant growth enhancement and crop fortification (9, 15, 16). Furthermore, this article focuses on illustrating the irrefutable and dual effects of ZSB on crops in terms of biofortification to improve the Zn status in the edible

parts by deciphering a functional interplay between ZSB and the plant.

## Concept of Biofortification: A Tactic for Curtailing Zn Malnutrition

Zinc is a “wonderful micronutrient,” necessary for all organisms, acted as a prosthetic group for approximately 3,000 proteins in animals and humans, and inimitable in numerous metabolic activities of plants such as (a) the activation of a series of miscellaneous enzymes (“RNA polymerases,” “carbonic anhydrase,” and “superoxide dismutase”) and (b) the formation and metabolism of biomolecules (proteins, carbohydrates, and lipids) (7, 17–20, 20). In plants, the deficiency of Zn decreases their growth, their ability to survive under stressful conditions, and finally the production of chlorophyll, which affect the plant health and its productivity (21, 22). With its amazing property, Zn deficiency is widely described as the main risk factor for developing diseases in humans. Various health-related disorders have been reported in response to Zn deficiency, such as growth disturbances, skeletal abnormalities, delayed wound healing, increased abortion possibilities, diarrhea (23), higher risk of infection, deterioration in physical growth, DNA damage, and cancer progression (1, 24). The accessibility of insufficient Zn in soils exists in the different regions of the world and includes India, China, Iran, Turkey, and Pakistan. These are the main regions where Zn deficiency exists in the human population (25). Another decisive factor is the lower solubility of Zn in the soil, which leads to the occurrence of Zn deficiency in crops. To counteract Zn malnutrition and maintain the elevated levels of this essential micronutrient, experts advocated the use of various strategies for the biofortification of Zn in crops. What is necessary in life is obviously food, although micronutrient-fortified food is the current demand in world agriculture. Hence, agronomic strategies, the plant breeding approach, the involvement of genetic engineering, and the application of ZSB are immensely practiced to produce a significant level of Zn in comestible parts of crops. Each approach has its own advantages and has some limitations as well. Agronomic biofortification practices through the use of fertilizers on the soil or the foliar application of Zn fertilizers to increase the Zn level in the plant foods, and thus nutrients-enriched food are consumed by the consumers (26, 27). In contrast, plant breeding has been practiced for several years as an important aspect of biofortification (5) to produce high-yielding varieties with a sufficient content of essential micronutrients such as Fe and Zn (4). Biofortification, resulting in particular from the genetic modification approach, is a time-saving approach for the development of nutritionally enriched crops. Secondly, this approach allows the transfer of a particular gene of importance (5). The production of “Golden Rice” illustrated as a significant model of biofortified crops develops *via* gene modification with the goal of accomplishing for beta carotene production. However, such aforementioned biofortification approaches are lucrative, featuring ethical issues, non-environmentally friendly (28), and irrelevant in those economically deprived nations where “rural-population” reside at large (29). The rampant use of synthetic fertilizers harms soil



ecology, disturbs the environmental balance, reduces soil fertility, pollutes groundwater, and ultimately has a negative impact on human health (30). Hence, there is an urgent need to develop a new cost-effective tactic for micronutrient biofortification. In this step, using agriculturally important microorganisms to bestow the fortification of plants as a viable auxiliary measure can deliver an improved level of requisite micronutrients in the comestible portions of plants and used these microorganisms as a substitute for fertilizers formulated by a chemical approach (6, 13, 31). Microorganisms involve in the imperative process of mineralization and solubilization of organic and inorganic materials (13, 32), hence they can be employed as bioelicitors in the translocation of multiple elements simultaneously in plants with higher crop yield. The integrated biofortification approaches are further depicted diagrammatically in **Figure 1**.

### ZSB: A Natural Biofortifying Agent

The use of ZSB as persuasive bioinoculants is a cost-effective method for Zn biofortification of food crops. ZSB dwelling in the rhizospheric region and the colonization of rhizospheres efficiently facilitate them as an auxiliary partner of the plant root for enhanced nutrient uptake in crops (12). As the chemical Zn fertilizers are implicated in soils, their conversion into an unavailable form of Zn compounds persists the problem of immobility of Zn from soil settings to plant tissues. This problem can be remedied by ZSB inoculants, which are able to solubilize the complex form of Zn in soils to better transport this nutrient from the soil to the plant (33). The mechanistic insight behind ZSB shows broad arrays of strategies for Zn solubilization such

as acidification (34), the production of metal chelating modules “siderophore” (10), “chelated ligands,” and the involvement of an oxido-reductive system (35, 36). However, the secretion of OAs through Zn solubilization by microbial agents is a key mechanism for Zn solubilization, in which two OAs (2-ketogluonic acid and gluconic acid) play an essential role in Zn mobilization (37). Only a few bacterial strains stimulating plant growth were examined for Zn solubilization and showed a positive influence on the relative parameters of plant growth (38). Rhizobacteria, which are located in the rhizosphere especially on the root surface (39), colonize this region immensely (40) and show some properties that promote plant growth. Therefore, such bacteria are formally described with a term “plant growth-promoting rhizobacteria” or abbreviated as “PGPR.” Several mechanisms namely phosphate (P) solubilization (41, 42), the secretion of siderophores (43, 44), hydrocyanic acid (HCN) (45, 46), the secretion of plant hormones, viz. indole acetic acid (IAA) [42., 36], gibberellins (47), and cytokinins (48) are the prime features of PGPR linked with efficient plant growth (49). Moreover, detectable improvements in growth (the enhancement in the shoot/root and total yield) and other improved attributes of plants such as natural ingredients and antioxidants after PGPR inoculation further illustrate them as “plant probiotics” (50–52). However, the use of ZSB with massive plant growth-promoting traits is a relatively new approach and offers a sustainable option to address the purpose of biofortification of staple foods (53). Stepwise *in vitro* studies begin with the isolation and screening of potential ZSB in the laboratory, leading to their more efficient use as bioinoculants for Zn mobilization

in field conditions. The *in vitro* screening of bacterial isolates on minimal media containing insoluble forms of Zn, namely zinc oxide (ZnO), zinc carbonate (ZnCO<sub>3</sub>), and Zn phosphate, is based on the formation of halo zones and the availability of the free form of Zn in liquid media (37, 54, 55), and the secretion of OAs (particularly gluconic acids) detected by liquid chromatography deciphering the Zn solubility potentiality of bacteria (56). Previous studies provide insights into microbial-assisted biofortification *via* some bacterial species for important food crops such as *Bacillus* sp. for wheat (8, 57), maize (58), soybean (8, 55), and rice (12), "*Pseudomonas fragi*," "*Pantoea dispersa*," "*Pantoea agglomerans*," *Enterobacter cloacae*, *Rhizobium* sp. for wheat (11), and "*Burkholderia*" and "*Acinetobacter*" for rice (59). ZSB increased the considerable Zn content in plants such as wheat (11), rice (60, 61), and maize (58) and also showed prolific effects on plant growth. A few studies that were conducted with ZSB in comparison to PSB required further investigations on Zn-solubilizing microflora from soil regions (rhizospheric soil, nutrient-rich soil, and nutrient-deficient soil) and plant regions (epiphytes and endophytes) as well as their further evaluation for improved Zn transport in plants to secure their candidacy as a natural biofortification agent. In addition, Zn-solubilizing inocula not only play their role in combating Zn malnutrition but also provide an alternative source of Zn chemical fertilizers to increase the concentration of Zn and other micronutrients in plants, especially cereals.

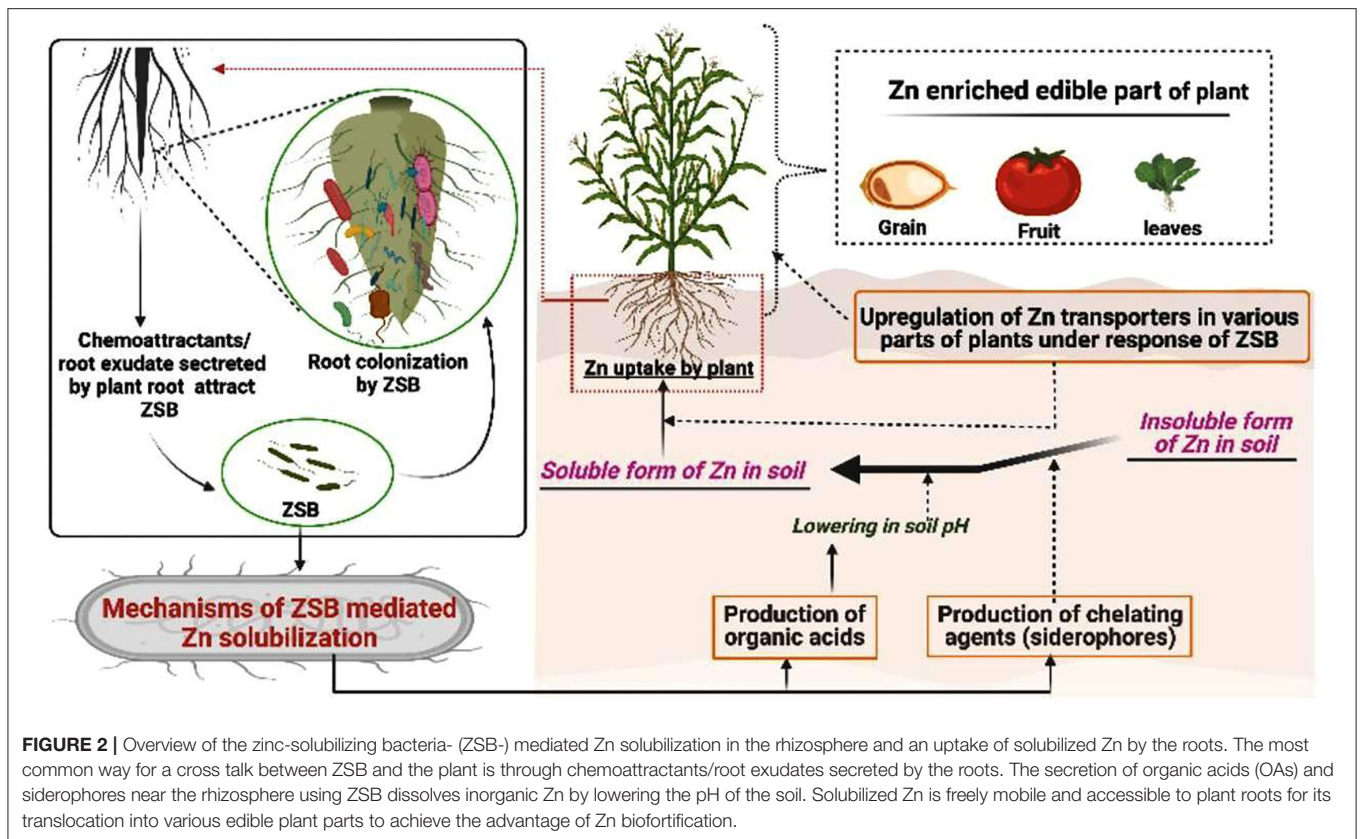
## Rhizospheric Region: A Hub for ZSB for a Direct Talk With the Host Plant

The term rhizosphere is defined as the living purview of the soil near plant roots that carries a unique population of microorganisms (62). It represents a hub for plant–microbe interactions (63), establishes a complex and dynamic ecological relationship between a microorganism and the plant, and supports a dense and diverse fauna (64, 65). In other words, the rhizosphere can be represented as a physical matrix containing the microbial population in an environment of roots where a network of chemical reactions through a wide range of metabolic activities produces multiple products that are beneficial to both plants and microorganisms. Plant metabolic activities influence the rhizosphere by releasing root exudates (66), which are either attractive or repulsive (67, 68) and determine the microbial diversity of the rhizosphere region (69). Besides root exudates, the cellular secretion in the form of various chemicals, *viz.* chemical compounds, antipathogenic metabolites, growth regulators, and nutrient mobilization are the other unique properties that belong to both plants and microbes. Root colonization is the major strategy of soil microorganisms that coexist in the rhizospheric region (70), and the collective bacterial population of this region is commonly referred to as rhizobacteria (71). The root colonization zone shows the mutual interaction between rhizobacteria and the root, with numerous compounds secreted by both plants and bacteria supporting the interaction between the root and the microbe. Therefore, signalomics is a more recent approach to metabolomics for identifying and profiling the

metabolites of both plant and microbial origin to decipher a chemical communication in the rhizospheric zone (72). However, root exudates act as communication signals that begin a biological and physiological communication between the soil microbiota and the roots by affecting the structural properties of the soil and associated microbial communities (73) and by promoting root surface colonization. ZSB as rhizobacteria are known for their potential to solubilize Zn through effective root colonization in response to the root exudates that act as chemoattractants for bacteria (12). Root exudation decides the microbial load and its survival in the rhizospheric hub (74). The competent role of rhizospheric bacteria in the recycling of nutrients, including carbon (75), nitrogen (76), phosphorus (42, 77), potassium (78, 79), and micronutrients (Fe, manganese, Zn, and copper) in the rhizosphere, continues to attract the significant attention of such bacteria in nutrient uptake and in promoting plant growth (39, 80–82). Several strategies of PGPR are directly attributed to the proliferation of plant growth. The secretion of metabolites by rhizospheric bacteria such as phytohormones, OAs, few enzymes for nutrient solubilization, siderophores, antibiotics, hydrolytic enzymes, antifungal compounds, and other compounds like osmoprotectants improve plant health and also eliminate the proliferation of soil pathogens in the rhizosphere region (39, 83, 84). The root colonization by ZSB and their mediated secretion of OAs/siderophores in the rhizospheric region solubilize the inorganic Zn in a free or solubilizing form, which can be easily taken up by plant roots and translocated into several parts including edible parts or grains as an additional microbial-assisted biofortification step (Figure 2).

## Endophytes: Who Is Inside the Plant for Micronutrient Biofortification?

"Endophytes" are special microbiota that live inside plants without showing pathogenic nature such as causing of disease (85) and colonize the internal plant tissues (86, 87). Endophytic microbiota are well documented to perform critical plant development, fitness, and diversification roles (88) and use the mechanisms similar to those shown by rhizobacteria for profound plant growth properties (86, 89). Multiple mechanisms, including nitrogen fixation (90), the synthesis of indole-3-acetic acid (IAA) (91), phytohormones (92–95), antimycotics (96–100), and siderophores (101–104) described the plant growth-promoting properties of endophytes (87, 105, 106). However, endophytes for micronutrient biofortification have hardly been studied in comparison to rhizobacteria (107, 108). Studies of Singh et al. (31), Rehman et al. (15), and (111) illustrated Zn biofortification in wheat by endophytes such as *Arthrobacter*, *Bacillus subtilis*, and *Pseudomonas* sp. A very few studies over the past decade have deciphered the essential role of endophytes in biofortification in combating malnutrition from micronutrients, particularly selenium (109, 110). A few microbial inocula also showed Zn biofortification in staple crops such as wheat (9, 31, 111, 112). Wang et al. (108) illustrated the increased level of Zn in rice in response



to two endophytes, namely “*Sphingomonas* sp. SaMR12” and “*Enterobacter* sp. SaCS20.” Endophytes use several multiple mechanisms to enable the uptake of nutrients in the edible portions of plants (113, 114). Zn-solubilizing endophytes may be a better biofortifying agent to increase the Zn localization in the eatable portion of wheat (9, 31), rice (108), and chickpea (16), thus presenting an alternative approach into the current strategies for biofortification. Besides Zn and Fe biofortification in plants, the two endophytic bacterial species of “*Arthrobacter*” exhibited a significant modification in root morphology and anatomy, which is a favorable phenomenon for better uptake of nutrients (111). *Piriformospora indica*, a fungal endophyte, with Zn treatment brought out the Zn fortification of lettuce leaves and also augmented the plant growth and chlorophyll levels in lettuce (115). It has been reported that the microbial consortia consisting of two endophytic strains (*Acinetobacter* sp. + *Bacillus* sp.) and mycorrhizal fungi increase selenium levels and also increase the antioxidant activity in wheat grains. The seed priming with Zn and *Pseudomonas* sp. also improved the overall productivity of wheat and Zn fortification of wheat grains (15). No further research has been published on investigating the interactions between plants and Zn-solubilizing endophytes and the functional properties of endophytes such as metabolite secretion and the mobilization/immobilization mechanisms associated with Zn solubilization. In-depth studies are required to further illustrate

the interior tissue’s colonization of the plant by endophytes and to determine their vital role in copious Zn translocation in plants.

### ZSB: A Promising Bioelicitor

Zinc plays an important role in all forms of life in terms of vitality and is involved in various metabolic processes. The plant enzymes such as carbonic anhydrase and superoxide dismutase are structurally linked to this crucial Zn micronutrient. The activities of these enzymes in plants are negatively affected in Zn scarred soil (116). Therefore, important food crops in cultivated land with a Zn deficiency are severely affected (117). Poor plant growth significantly lowers the overall productivity of the plants. It has been reported that several soil microorganisms solubilize insoluble Zn compounds and not only improve Zn translocation in plants, but also improve the yield-attributing properties of plants (53). Countless rhizobacteria, especially ZSB, have several probiotic plant traits that support plants by mobilizing the insoluble forms of Zn and contribute to increasing the crop yield. They are, therefore, often used as biofertilizers in sustainable agricultural practices (13). The selected ZSB strains showed their potential to boost yield-related traits *in vivo* (augmentation in length shoot, expansion of root, increment in total biomass of plant, chlorophyll content in the leaf, and improved grain yield of the crop), therefore these strains can be used as a competent bioelicitor

or more precisely as “biofertilizers.” Improving dry weight and seed weight at the time of maturation of the plants is also a significant potential of the ZSB (8). A noteworthy increase in yield attributed characters was observed for wheat (11), rice (12, 118), and maize (38) in response to ZSB inoculation. ZSB like *Bacillus* sp. (12), *Acinetobacter* sp., and *Burkholderia* sp. (59) helped plants with their overall growth and improved the uptake of Zn in straw and grains. ZSB strains have all the characteristics necessary to be promoted as proficient bioinoculants to diminish Zn micronutrient dearth in soils after proper field assessment and validation (8). Overall, ZSB has been identified as the main factor for integrated nutrient application in agriculture and therefore appears to have a viable potential for efficient use of such microorganisms to maximize crop production without showing harmful effects on the soil. Current approaches such as rhizosphere engineering, endophytic system enhancement, and the use of bacterial consortia are required to maintain the growth of the biofertilizer industry.

## Proposed Bacterial Mechanism Intended for Zn Biofortification

The mechanistic perspective behind bacterial-mediated Zn solubilization remains uncertain. They may likely have mechanisms similar to P-solubilizing microorganisms and Fe mobilizers through producing numerous compounds viz. OAs and chelating agents (119). To investigate the mechanisms of Zn solubilization, it is necessary to precisely outline individual or diverse mechanisms in the soil microorganisms that are necessary for the biogeochemical cycle of Zn. In addition, the solubilization of Zn is influenced by two bacterial processes such as either autotrophic or heterotrophic processes and also depends on the bacterial metabolism involved and the associated environmental conditions (56, 120). Autotrophic bacteria (including sulfur/ferric, Fe-oxidizing bacteria) have been extensively studied for their metal solubility potential and used in the recovery of Zn, nickel, and copper from industrial waste and ores (56, 121). On the contrary, heterotrophic bacteria with an immense ability to solubilize Zn have also attracted the attention of worldwide researchers and have been investigated in numerous agronomic studies as a bioinoculum to improve and localize Zn in the plant. Numerous known mechanisms are shown in Zn solubilization microorganisms. Mainly expected mechanism, which is elucidated as acidification, in which microorganisms produce OAs in the soil, which leads to the sequestration of Zn metal cations and a decrease in the affected soil pH (34, 56). Besides, the anions have the potential to chelate Zn (122). Additional probable mechanisms participated in Zn solubilization bacterially produced siderophores for the chelation of Fe and other metals (10), the secretion of chelated ligands, amino acids, vitamins, phytohormones, protons ( $H^+$ ) by microorganisms, and the inclusion of oxide reduction scheme on membranes of bacterial cells (35, 36, 123). Based on studies over the past few years, it has been assumed that, despite various possible mechanisms identified in ZSB, only

the phenomenon of OA secretion is an underlying microbial process for the solubilization of Zn. The accumulation of OA, particularly gluconic acid (and its keto derivatives) in tris-minimal broth medium (modified with an inexplicable form of the Zn source), which contains glucose as a single carbon source, definitely remains the most commonly described mechanism for Zn solubilization *via* the inoculated heterotrophic bacteria (37). The solubilization of inexplicable Zn compounds *via* bacterially secreted gluconic acid has been shown under *in vitro* conditions, e.g., for *Acinetobacter* (59), *Pseudomonas* (37, 124), and *Gluconacetobacter* (33). The major solubilization mechanism postulated in these *in vitro* studies was “acidification,” which resulted from the secretion of a significant amount of “gluconic acid” in the growth medium. The accumulation of this so-called “Zn solubilizing acid” in the microbial growth medium depends heavily on the availability of glucose in the current milieu of bacteria. Gluconic acid, synthesized from the extracellular or direct glucose oxidation *via* periplasmic glucose dehydrogenase (GDH, an example of the quinoproteins and redox co-enzyme) (125, 126). This enzyme is encoded by the *gcd* gene, and *pqq* operon encodes products such as “pyrroloquinoline quinone (PQQ)” (20, 127). A few studies suggested that the production of gluconic acid may not be compulsory for Zn solubilization as the different species of ZSB produce diverse arrays of other OAs. The Zn solubilization by the bacterium *Burkholderia cepacia* was ascribed to the secretion of four different OAs such as oxalic acid, tartaric acid, formic acid, and acetic acid, even when a single C source in the form of sugar (glucose) was present in the growth medium (128). In addition to the acids that are involved in Zn mobilization, siderophores are secreted by microorganisms as small organic compounds and are mainly involved in Fe solubilization *via* chelation processes (129). Some siderophores have also been reported to chelate Zn, but their precise role in Zn solubilization remains to be insufficiently considered (130, 131). Microorganisms secrete an ample variety of “siderophores” that are categorized into different types such as carboxylate type (i.e., “rhizobactin”), catecholate type (i.e., “enterobactin”), and hydroxamate type (i.e., “ferrioxamine B”) (132). Also, bacteria have been reported to secrete the special forms of this metal chelating compound that have a mixture of the most important valuable chemical groups (i.e., pyoverdine) (133). Soil microflora that colonize mineral surfaces are somehow different from the microbial inhabitants of the closest soil zone (134). Microbes on the surface of minerals create a microenvironment in which the microbes are protected from various stressful conditions (135, 136). Metal chelation occurs in the soil or is shared with the microenvironments of an adjoining microbial community (137). Siderophore-secreting bacterial populations from the soil dwellers promote the phenomenon of mineral solubility (138). Various mechanistic findings have been illustrated for the dissolution or chelation of minerals mediated by siderophores. However, a special focus was placed on the siderophore-mediated Fe solubilization (139). Siderophores are enormously efficient in solubilizing Fe and escalating the mobilization of metals (140). It can have an efficient affinity for a particular metal other than Fe (141).

**TABLE 1** | Upregulation of the ZIP transporters under the response of microorganisms.

Microbial agents	Plant	Upregulation of ZIP transporters	References
<i>Enterobacter cloacae</i> strain ZSB14	Rice	OsZIP1 and OsZIP5	(143)
Anonymous zinc solubilizing bacteria	Oat	OsZIP1, OsYSL2 and OsYSL6	(161)
<i>Arthrobacter sulfonivorans</i> DS-68 and <i>Arthrobacter</i> sp. DS-179	Wheat	TaZIP3 and TaZIP7	(111)
Coinoculation of <i>Trichoderma harzianum</i> (UBSTH-501) and <i>Bacillus amyloliquefaciens</i> (B-16)	Wheat	"TaZIP-1", "TaZIP-3", "TaZIP-5", "TaZIP-6", "TaZIP-7", "TaZIP-10", and "TaZIP-13"	(159)
<i>Pseudomonas fluorescens</i> Sasm05	Sedum (stonecrop)	SalRT1 and SaNramp1	(162)
Mycorrhizal fungi ( <i>Rhizophagus irregularis</i> )	Barley	HvZIP13	(158)
<i>Rhizophagus irregularis</i>	Barrel medic	MtZIP5 and MtPT4	(163)

## Current Insights on Molecular Aspects of Microbial-Assisted Zn Biofortification

In general, plant genomes comprise a wide range of genes with precise expression patterns in response to the uptake and transport of various types of micronutrients, which ensure that all tissues, especially the edible part, receive a satisfactory amount of vital nutrients necessary for the crucial activities of the cell. Some specific genes, especially ZIP family gene, have been discovered in the plants that play an imperative role in the transport and accumulation of Zn (142). The expression pattern of these genes is influenced either by high or low Zn concentrations (143). Under Zn deficiency conditions, however, the upregulation of the genes of the ZIP family was found in various plants (144). Rice was seen as a remarkable model for understanding the mechanisms of Zn transport with the 16 identified ZIP transporter members (144–146). Several genes (*AtZIP6*, *ZNT1*, *HMA2*, *HMA4*, and *OsZIP3*) (147) are significantly participated in Zn transport through the xylem or at the root and shoot site. In addition, the overexpression of such genes leads to an increased Zn movement in the shoot of plants (32, 148). Numerous ZIPs (Zn transporters) such as "OsIRT1", "OsIRT2", "OsZIP1", "OsZIP3", "OsZIP4", "OsZIP5", "OsZIP7", and "OsZIP8" have been explored in rice, which plays a major role in Zn translocation from the surrounding soil of the root to various sections of plants including mature seeds (143, 145, 146, 149, 150). Recently, a member of the ZIP *OsZIP9* (important influx transporter) located in the plasma membrane showed its contribution to the uptake of Zn in rice (151). *OsZIP* genes are expressed in roots, shoots, leaves, and spikelets under Zn-deficient conditions (144). It was shown that an expression pattern of a few ZIP genes (*OsZIP1*, *OsZIP4*, and *OsZIP5*) from rice is regulated by the accessibility of Zn<sup>2+</sup>, Fe<sup>2+</sup>, Cu<sup>2+</sup> and Mn<sup>2+</sup> (22, 143, 152). *ZmZIP* genes encoding ZIP transporters (*ZmZIP1–ZmZIP12*), especially in the maize genome assist in Zn uptake (153, 154). *ZmZIP5* and *ZmZIP11* are predicted for their productive contribution biofortification of maize (154). In wheat, the genes of the *TaZIP* family play a central role in the uptake of Zn and its transport in different plant regions (155). It

was found that the expression level of *TaZIP* transporters such as *TaZIP3*, *TaZIP5*, *TaZIP6*, *TaZIP7*, and *TaZIP13* is increased in the shoot and root part of wheat in the case of a Zn deficiency (156). *HvZIP* transporters in barley exhibited their significance for Zn uptake under Zn deficient conditions (157). As a bioinoculant, arbuscular mycorrhizal fungi (AMF) influenced the expression profile of some genes such as "*HvZIP3*," "*HvZIP7*," "*HvZIP8*," "*HvZIP9*," and "*HvZIP13*" and among these the higher expression of *HvZIP13* amplified the Zn uptake by the plant (158).

The gene expression analysis, which has been proven from recent studies, clearly showed that Zn-solubilizing microbial inoculants and other plant growth-stimulating microbes modulate the expression patterns of some of the genes from the Zn-regulated transporter family and thus played an important role in the transmission of Zn in the different parts of plants (143, 159). The co-inoculation of *Trichoderma harzianum* (UBSTH-501) and *Bacillus amyloliquefaciens* (B-16) augmented the expression level of the ZIP transporters genes ("*TaZIP-1*," "*TaZIP-3*," "*TaZIP-5*," "*TaZIP-6*," "*TaZIP-7*," "*TaZIP-10*," and "*TaZIP-13*") by 2.76–4.96-folds, which eventually led to increased Zn translocation in wheat cultivated in saline-sodic soil (159). Besides ZSB, mycorrhizal fungi also showed their contribution in biofortification (160). Under Zn deficient conditions, the mycorrhizal fungi (*Rhizophagus irregularis*) improved the Zn in the grain of *Hordeum vulgare* by upregulating the expression profile of *HvZIP13* (158). The resultant upregulation of the ZIP transporters under the response of microorganisms is illustrated in **Table 1**. Considerable advances have been made in interpreting an interplay between plants and microbes to enable the uptake of micronutrients from the soil into the plant. The production of OAs and metal chelators by microbes and the simultaneous expression of many ZIP transporters in plants can improve the uptake of Zn by plants. However, the cascade of events that takes place at the site of the plant–microbial interaction is very complex and is linked by a cross talk between microorganisms and plants, which needs detailed studies focusing on how microorganisms particularly ZSB are involved in the regulation of Zn transporter-associated genes.

## Scenario of Microbial Inoculants in Zn Exemplification in Plants

The cultivation of plants with a sufficient Zn concentration is the main need of the world today, so that the consequences of Zn deficiency can be overcome. In all countries, crops are the leading source of food for local residents. Grains, vegetables, and fruits fortified with Zn can effectively overcome Zn malnutrition. Therefore, the availability of the required Zn is an imperative factor in enhancing the overall crop yield (160, 164). The poor supply of Zn ultimately leads to the reduced productivity of the plants with an insufficient accumulation of Zn in their edible portions (165). ZSB were described as chief natural agents for Zn mobilization. Their interaction with the roots should improve the Zn status of the plant. The microbial-assisted biofortification opens up a newer and more environmental-friendly approach to agriculture, which relies less on chemical fertilizers (11, 27). Recent insights into plant–ZSB interactions revealed the potential of ZSB inoculants to address the Zn deficiency problem in plants. Such inoculants are living entities and are selected based on various attributes and employed for their valuable effect on crops in the following ways: (1) either by soil application or by seed treatment prior to sowing/transplanting; (2) monitoring by appropriate parameters for plant growth; and (3) the determination of the micronutrient level in cereals shows the microbially mediated biofortification. An increased level of Zn translocation occurs as a result of the root colonization by ZSB, which increases the pH of the rhizospheric soil through microbially secreted products (OAs) near the rhizosphere to perform Zn solubilization (53, 58). Furthermore, other organic compounds such as “siderophores” bind to metals, for example, Fe, and form a Fe(III)–siderophore complex at the exterior of mineral. This so-called complex form is then transferred to the adjacent soil environment to facilitate Fe uptake by local microbiota or plants (138, 166). Sufficient information is available to indicate a remarkable ability of ZSB to improve the bioavailability of Zn in the plant rhizosphere with adequate transport of this element to grains (53). As promising plant-probiotic agents, ZSB exhibit a strong influence on plant productivity. *Bacillus* sp. AZ6, with the capability to solubilize Zn with some plant-probiotic traits, exhibited an improvement in the biomass and length of the roots and shoots of the maize plant (38). Worldwide scientific studies validate a possible contribution of ZSB to the Zn biofortification of food crops by augmenting the Zn concentration in the edible parts of plants. In addition to the advantages of sustainable plant production, ZSB is considered to improve soil health. A wide range of ZSB, including both groups such as gram-positive and gram-negative bacteria, demonstrated their competence in biofortification. *Bacillus*, in particular, showed a profound role in Zn biofortification in numerous food crops (8, 12, 38, 55, 58, 167–172). The important crops such as maize (38, 54, 58, 173, 174), rice (59, 60, 171, 175, 176), and wheat (8, 11, 31, 32, 167, 177) have been studied extensively for Zn biofortification in response to ZSB inoculants as the grain parts from these crops offer the most important staple foods on a broad scale worldwide. A potential ZSB microbial strain, namely *Bacillus* sp.

enhanced the Zn translocation (%) in two different Basmati rice varieties, i.e., 22–49% (for *Basmati-385*) and 18–47% (for *Super-Basmati Rice*) (12). The study by Wang et al. (108) illustrated the role of “*Enterobacter* sp. SaCS20” and “*Sphingomonas* sp. SaMR12” in improving the Zn content in polished rice by 11.2% and 13.7%. Bacterium “*Rahnella* sp. JN6” improved the plant growth and increased Zn accumulation in *Brassica napus* (oilseed rape) in pot experiments (178). The strains of *Bacillus aryabhatai*, as prominent bioinoculants, amplified the Zn content in wheat grains (in the range of 42–61 mg/kg) compared to uninoculated control (8). (11) depicted the role of EPS producing ZSB strains influencing wheat plants, with inoculants such as *P. dispersa* EPS6, *P. agglomerans* EPS13, and *E. cloacae* PBS2, the dry weight of the shoots was increased, while the inoculation with *P. fragi* EPS1 showed a considerable increase in Zn content and dry weight of the root. ZSB with Zn source supplementation such as ZnO, ZnSO<sub>4</sub> also provided fruitful benefits of promoting plant growth, soil health, and Zn biofortification. (174) reported the enhancement in plant growth and soil fertility under the response of a bioinoculant (*E. cloacae*) and Zn supplement (ZnO). Moreover, the rice plant growth was improved by *Acinetobacter* sp. (TM56) and ZnSO<sub>4</sub> (176). Compost, enriched with *Bacillus* sp. AZ6 and ZnO, showed a profound effect on plant growth, crop yield and subsequently improved the Zn supply in paddy grains via a slow release of Zn from ZnO (171). With ZnO supplementation, Zn-solubilizing bacterial strain *Gluconacetobacter diazotrophicus* showed a remarkable nutrient uptake in maize (179). The response of the bacterial consortium (*E. cloacae* + *Bacillus megaterium*) with Zn sulfate additives augmented the Zn uptake in wheat grains and showed the utmost range of soil exchangeable Zn (180). Goteti et al. (54) showed that the inoculation of maize seeds with ZSB (“*Pseudomonas* sp. P29,” “*Pseudomonas* sp. P33,” and “*Bacillus* sp. B40”) augmented the dry weight of the plants with improved Zn accessibility. The study of Vaid et al. (59) on ZSB (*Acinetobacter* sp. and *Burkholderia* sp.) showed growth attributes of the rice plant in terms of an increment in the number of panicles, productive tillers, dry matter, straw yield and grain yield, and dry matter yield. In addition, the same study also showed the suitability of ZSB for biofortification by enhancing the level of Zn content in grains. Inoculation with *Bacillus cereus* increased the Zn concentration in soybean seeds. On the contrary, the reduced phytate content of the seeds showed the bacterium’s ability to reduce the effects of an anti-nutritional factor (167). Contemporary studies have deciphered the ZSB-mediated Zn biofortification in food plants. However, the role of consortia containing Zn-solubilizing microorganisms in Zn biofortification is not fully revealed. The microbial consortia accelerate plant growth compared to a single microbial inoculum (39, 66). “Rhizospheric–endophytic mix inoculants” bearing immense plant-probiotic traits increase the plant biomass and also improve the assimilation of micronutrients in cereals (181). The plant-probiotic consortia also depict the efficient disease suppressive effect, thus reducing plant mortality (182). Bacterial consortium can have a revitalizing effect on plants as various kinds of bacterial strains can work synergistically to provide nutrients and eliminate inhibitory products (183, 184).



The development of efficient bacterial consortia has an indispensable place in biofertilizer-based research and their potential applications in sustainable agriculture (185). The development and formulation of ZSB consortia can offer several key advantages:

- The use of ZSB consortia can offer more advantages in Zn biofortification compared to the individual ZSB inoculum.
- ZSB consortium as a natural resource can combat Zn deficiency.
- The use of the ZSB consortium can reduce the uncontrolled use of chemical fertilizers.
- ZSB consortium can show the massive plant growth-promoting properties.
- ZSB consortium can act as competent “plant-probiotic” to enhance the crop yield.

The microbial consortium of *Burkholderia* and *Acinetobacter* improved the Zn content and its bioassimilation in wheat grain and wheat straw (186). A consortium of Zn-solubilizing *Bacillus* species (*Bacillus* sp. SH-10 and *B. cereus* SH-17) fortified rice through “microbial-assisted biofortification strategy” showed the highest Zn translocation index (1.6 to 1.7) (12). The highest Zn level in grains, i.e., 16.1 and 16.0 mg/kg, was measured in two rice varieties “PD16” and “NDR359,” which were inoculated with the Zn-solubilizing bacterial consortium (*Burkholderia* and *Acinetobacter*) (59). The co-inoculation of *Enterobacter* and *Serratia marcescens* significantly improved the Zn content in wheat by 23% and 32% under field and pot trial studies, respectively (11). This consortium also enhanced the concentrations of Cu, Mn, and Fe under the pot trial by 56, 52, and 18% and in the field studies by 43, 48, and 16%, respectively. The consortium with two compatible bacterial strains, “*Pseudomonas jessenii* (R62)” and “*Pseudomonas synxantha* (R81),” showed a significant influence on Zn uptake in rice seeds (187). The study of Tariq et al. (60) demonstrated the efficiency of a Zn-solubilizing bacterial consortium (*Pseudomonas* sp. and other PGPR strains) to increase Zn content (up to 157%) in rice. Zn accumulation ( $107.01 \mu\text{g g}^{-1}$ ) in flag leaf was taken into account during inoculation with an *Anabaena-Azotobacter* biofilm, thus illustrating the cyanobacterial-assisted Zn biofortification in maize (188). A consortium of three bacterial strains (*B. megaterium*, *A. chlorophenicus*, and *Enterobacter*) improved Zn content (58.5 and 62.8% increment under the pot and field trial, respectively) in *Triticum aestivum* L and showed a considerable amount of other bioavailable micronutrients like Cu, Mn, and Fe (189). In addition to the advantages of biofortification, the use of microbial consortia also indicated a positive impact on various yield-related parameters such as gain in thousand-grain weight, number of tillering per plant, and grains per ear (190). Moreover, the contribution of blue-green algae in biofortification was also determined. The consortium (*Anabaena* sp. CR1 + *Providencia* sp. PR3) with 75% RDF (recommended dose of fertilizers) showed an improved level of Zn uptake (323.8 g/h) in wheat (191). Recently, the

metagenomics-based study revealed the existence of potential Zn-mobilizing species, particularly *Massilia* and *Pseudomonas* sp., that could form a functional community in increasing Zn concentration in grains of wheat varieties (192). More recent studies that decipher the microbial-assisted improvement in the plant yield and Zn content of crop plants are listed in Table 2.

## Challenges of Getting Zn Nutrition and Fortification by the Field Application of ZSB

*In vitro* screening of ZSB executes a task of developing ZSB-based inoculants, however, the selection of potential ZSB strains and their formulation is a challenge in itself. Additionally, the use of ZSB-based biofertilizers can also be challenging due to the inconsistency under field conditions, so the results in field studies do not appear as good as they would under controlled conditions. Crops show a slow response toward biofertilizers, and sometimes it becomes unsuccessful as the inoculum takes the time to build up its population and root colonization. Due to these circumstances, it leads to a low acceptance of microbial-based fertilizers by farmers (197).

However, the following points illustrate the main challenges of ZSB application under field conditions:

- a) *The decrease in the effectiveness of bioinoculants may be due to the physical and chemical properties of the soil.*
- b) *Environmental factors determine the activity of the bioinoculants used as various factors such as drought, salinity, alkalinity, acidity, and high concentrations of heavy metals (such as Cd, Hg, and Cr) in the soil can reduce the performance of ZSB-based bioinoculants in the soil.*
- c) *The massive use of synthetic chemicals and their harmful residual effects can reduce the activity of certain bioinoculants.*
- d) *The successful field application of ZSB-based bioinoculants relies on the climatic factors required for a particular crop.*
- e) *The inability of an bioinoculant to effectively colonize the rhizosphere due to its small abundance and its competition with the pre-existing indigenous microbiota.*
- f) *Soil type, pH, radiation, temperature, nutrient accessibility, oxygen concentration, and the extent of interaction with the native soil microorganisms, etc., all affect the plant-bioinoculant interaction and affect their survival in the host plant.*
- g) *Improper exudation of OAs and siderophores in the soil after the application of bioinoculants can reduce the uptake of Zn by plants.*
- h) *The resulting higher phytic acid content in the edible parts of plants impedes the bioavailability of Zn, and hence significantly limiting the advantages of biofortification.*

However, it is strongly recommended that the exploration and use of region-specific Zn-solubilizing microbial strains show the highest effectiveness for Zn biofortification. Instead

**TABLE 2** | Benefits of zinc-solubilizing bacteria (ZSB) in plant growth promotion and zinc (Zn) biofortification in important food crops.

Bacterial strains/treatments	Plant	Benefits to plant	Amount of zinc in edible part	References
<i>Bacillus megaterium</i>	Chili pepper	Enhanced plants growth, nutrient uptake and yield	0.25 mg/100 g	(172)
1.5% zinc-lysine chelate + <i>Alcaligenes</i> sp., <i>Bacillus</i> sp., and <i>Pseudomonas</i> sp.)	Maize	Improvement in cob diameter and cob length, grain weight	8.30 ppm	(193)
<i>B. aryabhatai</i> ZM31 + <i>B. subtilis</i> ZM63	Maize	Improvement in the plant growth, cob length and dry weight, and grain nutrient concentrations	52.0 mg/kg	(170)
<i>Pseudomonas</i> spp.	Okra	Effective on plant growth promotion and the enhancing Zn content in the Okra fruit	2.85 mg/100 g	(194)
<i>Pseudomonas</i> sp. VBZ4	Tomato	Taller plants with wider stems, higher biomass of plant with an increased number of tomato fruit	2.87 mg/100 g	(195)
<i>R. tropici</i> + <i>B. subtilis</i>	Common bean	Improvement in shoot dry matter and grain yield	60.7 mg/kg	(168)
<i>Bacillus subtilis</i> QST713	Wheat	Increment in the concentration of P and Zn in grains and Zn harvest index	41 mg/kg	(169)
<i>Bacillus altitudinis</i>	Chickpea	Improvement in plant growth promotion parameters	60 mg/kg	(164)
<i>Trichoderma harzianum</i> UBSTH-501 + <i>Bacillus amyloliquefaciens</i> B-16	Wheat	Enhanced salt tolerance level, increased plant growth and also improved total grain yield	60.33 $\mu\text{g g}^{-1}$	(159)
<i>Bacillus subtilis</i> + AM fungi	Wheat	Increased macronutrient (nitrogen and phosphorus) and micronutrient (iron and zinc) content in wheat grains, improved yield related parameters	50.7 mg/kg	(190)
<i>Rhizobium radiobacter</i>	Lettuce	Increment in all plant growth related parameters along with improved nutritional content	80.36 mg/kg	(196)

of using ZSB directly as an inoculum, it makes sense to use a suitable carrier. The ZSB should have an additional characteristic for phytase production as phytase can reduce the concentration of an antinutritional factor (phytic acid) and increase the availability of Zn. The microbial groups that may play a vital role in the nutrient cycle in soils are very diverse, and bacterial-mediated Zn solubilization is seen as the main strategy for Zn nutrition in plants. However, a very large section of the soil microbiota is still unexplored, as around 99% of the microorganisms living in the soil cannot be cultivated (198). Thus, culture-independent tactics are necessary to decipher the functional attributes of native microbiome involved in Zn solubilization in soils. Molecular approaches of culture-independent methods for determining the functional gene or microbial diversity in soil have been developed considerably in the recent past. Metagenomics also offers new perspectives to identify the existence and abundance of certain microorganisms or functional genes specific for soil Zn mobilization or increasing root Zn uptake, mainly the synthesis of OAs and siderophores (192).

## CONCLUSION

Many ZSB have attracted significant attention for their ability to endorse Zn assimilation in plants through direct mechanisms (Zn solubilization and its transportation) by acting as natural biofortifying agents. Mechanism adapted by ZSB for the growth of plants is similar as of ordinary plant growth-elevating bacteria either studied from the rhizosphere or inner tissues of plants. However, the mechanistic view of ZSB is quite different from PGPR. For example, the occurrence of OA production offers the ZSB an opportunity to solubilize insoluble Zn in the soil and make Zn accessible to plants. The interaction of ZSB with plants can be an indicant of positive relationships where microbial-mediated plant growth-promoting effects meliorate the healthy lifestyle of host plants. There is still huge vague in our understanding of the interaction of bacteria with the host plant residing in the rhizospheric zone or as part of phytomicrobiont turning the inexplicable Zn into soluble Zn form, and as a channel, these ZSB facilitate increased Zn content in different plant parts. Not much study was performed on ZSB-based biofortification

consequently inciting to create a systematic way for unveiling the functional aspects of bacterial genes participated in Zn and other micronutrient solubilization and beneficial interaction of ZSB with plants. The functional genomics, proteomics, and metabolomics approach may in the near future be able to construct ZSB formulations to find out their competence in increasing multiple micronutrients in the edible plant parts for a more sustainable remedy of nutrient deficiencies. However, more work is still required for ZSB from soil and plants, and the development of ZSB biofertilizers for future use in crop biofortification.

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VU: writing of original draft of manuscript. All authors: conceptualization, editing, and approval of submitted version.

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