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Contemplating the role of zinc-solubilizing bacteria in crop biofortification: An approach for sustainable bioeconomy

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Modern agriculture pays attention to improving agricultural production by producing zinc-enriched crops through zinc-solubilizing bacteria to strengthen the bioeconomy. Zinc deficiency in the soil reduces plant growth and also leads to less uptake of zinc in the edible portion of plants. Therefore, the zinc content in the edible parts of plants can be increased through the biofortification approach. However, most of the biofortification approaches are laborious and need expensive input in routine practices. Therefore, the microbiological biofortification approach may be beneficial in increasing the zinc concentration in plants and improving crop quality with the ultimate benefit of a greener path. The use of microbes may thus be favorable for elevating zinc content in plants and enhancing crop quality, ultimately providing a summation of the role of microorganisms for a greener strategy. In addition, the application of zinc-solubilizing bacteria as a potential biosource represents a cost-effective and alternate biofortification strategy. Zinc-solubilizing bacteria act as natural bio-fortifiers that can solubilize the unavailable form of zinc by secreting organic acids, siderophores, and other chelating compounds. This review thus focuses on zinc-solubilizing bacteria for plant biofortification and their contribution to enhance crop yield and the bioeconomy in a more sustainable manner.

KEYWORDS
zinc-solubilizing bacteria, biofortification, bioeconomy, zinc, crop

Introduction

The zinc (Zn) deficiency problem in food crops can be addressed through the zinc biofortification approach to provide adequate zinc content in multiple edible parts of plants (Upadhayay et al., 2022a; Upadhayay et al., 2022b). Plant zinc uptake sometimes drops due to adverse environmental factors, resulting in reduced plant growth. In addition to improving crop production and yield, global research focuses on nutritionally enriched crop development and the commercialization of bio-fortified crops to prevent micronutrient-related malnutrition. Cakmak (2008) explained that zinc is a necessary micronutrient for the metabolic activities of plants, animals, and microorganisms. The deficiency in zinc and other micronutrients, such as iron and selenium, is known as "hidden hunger" (De Valença et al., 2017). Consequently, micronutrient deficiencies increase the risk of malnutrition in the global population (Upadhayay et al., 2018). Zn deficiency is as important as iron (Fe) and vitamin A deficiency in terms of health-related risk factors worldwide (Salgueiro et al., 2000; Hotz, 2007; Palmgren et al., 2008). Zn scarcity affects a large portion of arable land, and about a third of the human population suffers from zinc malnutrition due to poor Zn intake (Cakmak, 2002). Therefore, many programs have been proposed to circumvent zinc and other micronutrient deficiencies (White and Broadley, 2011). In this regard, the biofortification concept is an efficient method to increase essential bioavailable nutrients, including zinc, in crops through the application of agronomic practices (zinc fertilization) and plant breeding (White and Broadley, 2005; Mayer et al., 2008). Another approach employs zinc-solubilizing bacteria as potential bio-inoculants for improved crop Zn uptake. Plants establish multifaceted relationships with microbial communities, in which a wide range of microbial organisms form a "microbiome" in a specific niche. The microbiome improves nutrient uptake, protects plants from biotic (pathogens) and abiotic stresses, and alters their metabolic abilities (Mitter et al., 2013). The characterization and manipulation of a plant microbiome can improve crop production and reduce the need for pesticides and fertilizers, thereby improving sustainable crop production. The plant growth-promoting rhizobacteria (PGPR), which have a strong association with roots in the rhizosphere, enhance plant growth through a broad spectrum of plant growth-promoting activities, including phosphate solubilization, nitrogen fixation, secretion of Fe-chelating "siderophores", extracellular enzymes, phytohormones, ammonia, and exopolysaccharides (Kloepper et al., 1991; Ahemad and Kibret, 2014; Backer et al., 2018). The use of zinc-solubilizing bacteria with diverse abilities to promote plant growth is the current need to increase crop productivity and food security (Hussain et al., 2018). A few studies have explored the outstanding ability of zinc-solubilizing bacteria (ZSB) to increase the zinc concentration in the edible parts of crops (Moreno-Lora et al., 2019; Bhatt and Maheshwari, 2020; Mumtaz et al., 2020; Verma et al., 2020; Bashir et al., 2021; Jalal et al., 2021; Karnwal, 2021; Kushwaha et al., 2021; Upadhayay et al., 2022a; Upadhayay et al., 2022b). The use of agrochemicals has led to (a) a loss of soil fertility, (b) risks to human health, (c) an imbalance in the environment, (d) a change in soil ecology, etc. Therefore, switching to organic farming practices is an effective way to mitigate the detrimental effects of the intensive use of agrochemicals. The use of bio-based products such as biofertilizers, biopesticides, and organic additives is beneficial in increasing crop productivity and provides an eco-friendly approach to sustainable agriculture. Furthermore, strengthening the bioeconomy is a major concern in the agricultural sector. Hence, there is a need to strengthen the financial situation of farmers through less input with increased crop productivity by adapting the concept of green agricultural practices. The bioeconomy in the agricultural sector can include the use of biological-based processes such as the exploitation of agriculturally important microorganisms and their use as biofertilizers and biopesticides. The use of such biostimulants has the potential to contribute significantly to the so-called bioeconomy, which will ultimately lead to a more long-term sustainable agricultural development and enhanced food security (Rengalakshmi et al., 2018). Therefore, challenges need to be addressed to strengthen the bioeconomy through improved crop productivity with zinc-enriched grains or other edible plant parts in response to zinc-solubilizing bacterial inoculants. The present article illustrates the dual effects of ZSB on food crops in terms of biofortification to improve the Zn status in the comestible portions and the sustainable use of ZSB to improve the bioeconomy by increasing the quality and productivity of food crops.

Zinc malnutrition

This important micronutrient plays a very vital role for both plants and animals and shows its essence in the form of a cofactor for more than 300 types of enzymes. Zinc deficiency is caused by insufficient Zn intake and its inadequate bioavailability. Hence, a lower intake of the dietary form of Zn has led to several health problems in low-income countries. Besides this, Zn also plays a crucial structural role in various proteins (*e.g.*, transcription factors). It is needed to maintain the vitality of humans, plants, and microorganisms. In plants, carbonic anhydrase activity relies on adequate levels of zinc, and Zn is also required for the biosynthesis of chlorophyll and protein, enzyme activation, oxidation reaction, and carbohydrate metabolism (Xi-wen et al., 2011; Hussain et al., 2018). Furthermore, the lack of this element causes the retardation of several processes, such as photosynthesis and the synthesis of biomolecules (carbohydrates, RNA, and proteins), which leads to reduced quality of the crop (Efe and Yarpuz, 2011; Hussain et al., 2018). Therefore, the use of zinc fertilizers has become crucial for improving the quality and performance of the crop. The World Health Organization has listed this micronutrient in the category of major risk factors responsible for several human diseases (WHO, 2002). Several ailments develop in response to zinc deficiency, including delayed wound healing, diarrhea, growth retardation, increased risk of infection, and abortion. Apart from that, DNA damage and the progression of cancer are also associated with zinc deficiency (Salgueiro et al., 2000; Gibson, 2006; Prasad, 2008). Various countries, such as India, Iran, Pakistan, Turkey, and China, have a vast area of zinc-deficient soil and present a valid reason to induce the consequences of zinc dearth in the human population of these specific regions (Cakmak and Kutman, 2018; Upadhayay et al., 2019). Furthermore, inadequate zinc solubility in the soil is a major reason for the onset of zinc deficiency in crops (Upadhayay et al., 2018; Upadhayay et al., 2019; Upadhayay et al., 2022b).

The idea of biofortification to counteract Zn-associated malnutrition

Various biofortification strategies have been described to counteract micronutrient malnutrition (Hussain et al., 2018; Upadhayay et al., 2018). The concept of biofortification is a suitable way to biofortify crops with elevated concentrations of micronutrients such as zinc, iron, and selenium (Kamran et al., 2017; Upadhayay et al., 2018; Upadhayay et al., 2022a; Upadhayay et al., 2022b). Selective biofortification strategies include an agronomic approach, genetic engineering, plant breeding, and the application of biostimulants (plant growth-promoting bacterial inoculants) (Upadhayay et al., 2018; Khan et al., 2019; Upadhayay et al., 2022a). These crop biofortification strategies have been extensively studied and reported to increase the concentration of micronutrients in the edible parts (grains, fruits, and leaves) of plants. In the agronomic approach of biofortification, the nutrient-rich fertilizers are applied to the foliage part of plants or incorporated directly into the soil (Upadhayay et al., 2022a).

This approach increases the micronutrients in the edible portion of plants. Zinc fertilizers such as zinc sulfate are added to the soil or applied as a foliar spray to augment the zinc levels in various plants to achieve the benefits of biofortification (Cakmak and Kutman, 2018). Studies have also reported an increase in the growth and yield of plants with improved zinc levels in the edible parts of plants (White and Broadley, 2005). Conventional breeding strategies and genetic engineering approaches to improve micronutrient density in edible crops are popular (Upadhayay et al., 2018; Upadhayay et al., 2022a). Importantly, biofortification through genetic modification is time-consuming but produces crops with significant levels of micronutrients in the edible parts of plants (Garcia-Casal et al., 2016; Upadhayay et al., 2018). However, these biofortification strategies are costlier and an inapt option in nations hosting a large proportion of the rural population (Mayer et al., 2008; Upadhayay et al., 2018; Upadhayay et al., 2019). The rampant application of chemical fertilizers affects soil fertility, disrupts soil ecology, and negatively impacts the environment (Joshi et al., 2006; de Santiago et al., 2011; Upadhayay et al., 2018; Upadhayay et al., 2019). Therefore, economically feasible strategies that could be fruitful in increasing the zinc content in the edible portions of plants are required (Bouis, 2003). Moreover, as a substitute for chemical fertilizers, the use of zinc-solubilizing bacteria can be encouraged since these bacteria are living transformers to convert unavailable forms of zinc into accessible forms (Rana et al., 2012; Singh et al., 2017; Upadhayay et al., 2018; Upadhayay et al., 2019). The ZSB facilitates this process by the secretion of organic acids, and therefore the dissolved form of zinc is taken up by plants (Hussain et al., 2018). These ZSB also improve the quality of the crop through a wide range of mechanisms, including nutrient solubilization, production of siderophores and exopolysaccharides, and other plant growth-promoting traits (Kamran et al., 2017; Hussain et al., 2018). At this point, zinc-solubilizing bacteria can be used as an efficient bio-inoculant to ensure an adequate zinc supply in the edible parts of food-based crops in a more eco-friendly way.

Bacterial role in zinc biofortification

Zn biofortification of food crops using bio inoculants is a cost-effective method (Upadhayay et al., 2022a). When ZSB is present as well as colonized in the rhizosphere, it acts as an adjunct collaborator for the plant root to accelerate the uptake of nutrients from the soil (Shakeel et al., 2015). As Zn fertilizers are used in soils, their conversion into inaccessible Zn compounds perpetuates the immobility of Zn from soil to plant tissues (Sharma et al., 2013). ZSB inoculants can alleviate the problem by solubilizing the complex form of Zn in soils, allowing it to be transported more efficiently from the soil to the plant (Saravanan et al., 2007; Upadhayay et al., 2022a). The mechanistic understanding of ZSB encompasses some Zn solubilization strategies, like acidification by producing organic acids (Kamran et al., 2017), the synthesis of metal chelating modules called "siderophore" or "chelated ligands", and the engagement of an oxidation–reduction system (Singh et al., 2018; Upadhayay et al., 2018; Upadhayay et al., 2022a). Only a few studies on the Zn solubilizing capability of rhizospheric bacteria and endophytes as well as their effects on plant growth are documented. Rhizobacteria are well-known microbes that especially reside and colonize in the rhizosphere and exhibit multiple properties related to plant growth, such as phosphate dissolution, potassium solubilization, production of siderophore, exopolysaccharides, phytohormones (indole acetic acid, gibberellins, cytokinins, *etc.*), and HCN (Ahemad and Kibret, 2014; Backer et al., 2018). Moreover, endophytic bacteria, a category of bacteria that reside in plant tissues, have a positive effect on plant growth and development (Afzal et al., 2019). Hence, these bacteria are referred to as "plant growth-promoting bacteria" in a scientific context. Such bacteria can be considered probiotics for plants since they contribute to increases in shoot/root length, dry matter accumulation, grain yield, and natural components of plants (Menendez and Garcia-Fraile, 2017).

The use of ZSB, having numerous plant growth-promoting properties, presents a new strategic plan for developing biofortified crops in an eco-friendly manner (Upadhayay et al., 2022a). The remarkable zinc solubilization behavior and plant growth-stimulating properties of a bacterial strain tested under *in vitro* settings make it a suitable bio-inoculant for increasing the zinc content in plants (Vaid et al., 2014; Kamran et al., 2017; Upadhayay et al., 2022a; Upadhayay et al., 2022b). Upadhayay et al. (2022b) illustrated the solubilization behavior of the insoluble form of Zn (ZnO) in solid and liquid media under laboratory settings. Few studies have decoded the relevance of organic acids produced by bacteria in zinc solubilization (Fasim et al., 2002; Saravanan et al., 2007; Costerousse et al., 2017; Mumtaz et al., 2017; Hussain et al., 2018; Upadhayay et al., 2022a; Upadhayay et al., 2022b). Some zinc-solubilizing bacterial strains of *Bacillus* have been shown to play their roles in zinc biofortification of some food-based crops: *Bacillus aryabhattai* (Ramesh et al., 2014), *Bacillus subtilis* QST713 (Moreno-Lora et al., 2019) for wheat, consortia of *B. aryabhattai* ZM31 and *B. subtilis* ZM63 for maize (Mumtaz et al., 2020), and *Bacillus altitudinis* for chickpea (*Cicer arietinum* L.) (Kushwaha et al., 2021). Recently, the study of Upadhayay et al. (2022b) demonstrated the role of *Burkholderia cepacia* and *Pantoea rodasii* in the biofortification of rice grains. Moreover, the Zn- and P-solubilizing bacterium "*Rhizobium radiobacter* (LB2)" improved lettuce crop growth and Zn nutrition quality (80.36 mg/kg zinc content in leaf) in saline soil. Zn-solubilizing endophytes may indeed be a good biofortifying agent to enhance the Zn localization in the eatable portion of wheat (Rehman et al., 2018), rice (Wang et al., 2014), and chickpea (Ullah et al., 2020), thereby introducing an alternative strategy for biofortification (Upadhayay et al., 2022a). In recent research, gene expression analysis was used to demonstrate that Zn-solubilizing microbial biostimulants, along with other plant growth-stimulating microbes, influence the expression profiles of some of the Zn-regulated transporter family genes and, as a result, play a key role in the transport of zinc to the various plant parts (Krithika and Balachandar, 2016; Upadhayay et al., 2022a). The co-inoculation of *Trichoderma harzianum* and *Bacillus amyloliquefaciens* led to a 2.76–4.96-fold increase in the expression of the ZIP transporter gene in wheat, which resulted in enhanced zinc transport (Singh et al., 2021). In addition to addressing zinc deficiency, Zn-solubilizing microorganisms can also be used to enhance the productivity of food crops.

Mechanistic overview of zinc solubilization

The risk associated with zinc malnutrition is the poor supply of zinc from soil to the plant. However, the soil is well-off with an abundance of zinc, but its dearth in crops prevails because of an inaccessible form of zinc in the soil (Sunithakumari et al., 2016). The production of organic acids has determined the critical mechanisms of nutrient solubilization by microorganisms as the most imperative mechanism of phosphate solubilization. The production of organic acids (Saravanan et al., 2004) and siderophore (as chelating agents) has been determined as the principal mechanism for the solubilization of zinc by ZSB (Upadhayay et al., 2018; Upadhayay et al., 2022a; Upadhayay et al., 2022b). The means of zinc solubilization are very similar to those of P solubilization (Upadhayay et al., 2022a). Moreover, autotrophic and heterotrophic processes can affect the pattern and process of Zn solubilization and depend on the type of bacterial metabolism and environmental settings (Costerousse et al., 2017; Upadhayay et al., 2022a). Autotrophic bacteria, *e.g.*, sulfur/iron (III) and iron (Fe)-oxidizing bacteria, have been investigated for metal solubilization and thereby used for the recovery of metals (Zn, Ni, and Cu) from industrial waste and ores (Schippers et al., 2014; Costerousse et al., 2017). For the past decade, heterotrophic bacteria that solubilize Zn and promote plant growth have been studied for improved plant productivity and significant Zn accumulation in the edible parts of plants after their inoculation (Costerousse et al., 2017; Gontia-Mishra et al., 2017; Kamran et al., 2017; Mumtaz et al., 2017; Idayu Othman et al., 2017; Saravanan et al., 2007; Ramesh et al., 2014; Vaid et al., 2014; Upadhayay et al., 2022b; Vidyashree et al., 2018).

Organic acid production is the most significant mechanism for zinc solubilization. Bacterial strains secret organic acids and bring down the pH of nearby soil (Costerousse et al., 2017; Kamran et al., 2017; Upadhayay et al., 2018; Upadhayay et al., 2022a; Upadhayay et al., 2022b). It is generally accepted that gluconic acid and its derivatives dissolve insoluble forms of zinc, such as zinc phosphate, zinc carbonate, and zinc oxide, into soluble/available forms of zinc (Fasim et al., 2002; Saravanan et al., 2007). Different microbial strains including *Gluconacetobacter, Pseudomonas, and Acinetobacter* have been already reported to produce a massive amount of gluconic acid ascribed for Zn solubilization (Di Simine et al., 1998; Fasim et al., 2002; Saravanan et al., 2007; Vaid et al., 2014). However, *Burkholderia cepacia* solubilized zinc through other organic acids (oxalic, formic, tartaric, and acetic acids) rather than gluconic acid (Li et al., 2009). Other possible mechanisms that probably contribute to zinc solubilization are the production of siderophores, amino acids, chelated ligands, vitamins, proton, and oxido-reductive systems on cell membranes (Chang et al., 2005; Saravanan et al., 2011; Hussain et al., 2018; Upadhayay et al., 2018). Excretion of protons (H^+) by Zn-solubilizing microorganisms can lead to acidification of the rhizosphere region and thus results in the increased availability of Zn and other micronutrients (Upadhayay et al., 2018; Upadhayay et al., 2019; Upadhayay et al., 2022a). "Zn chelation" is also an effective mechanism of Zn-solubilizing bacteria to meet the requirement of increased Zn levels in plants (Hussain et al., 2018; Upadhayay et al., 2018).

The bioavailability of zinc in the root zone or rhizospheric zone can be augmented by incorporating zinc-chelating compounds (Obrador et al., 2003; Singh and Prasanna, 2020). "Zn chelator metallophores" secreted by three bacterial strains such as *Microbacterium saperdae*, *Enterobacter cancerogenes*, and *Pseudomonas monteilii* have been reported to augment the Zn bioavailability in soil and its enhanced uptake by the roots (Whiting et al., 2001). Tariq et al. (2007) illustrated the effect of the natural chelating agent "ethylenediaminetetraacetic acid" by biofertilizers (containing bacterial strains such as *Azospirillum lipoferum*, *Pseudomonas* sp., and *Agrobacterium* sp.) on the solubilization of insoluble Zn salts. The production of siderophores is also considered a possible Zn solubilization mechanism (Saravanan et al., 2011); these are the organic compounds with low molecular weight synthesized by microorganisms under iron-deficient conditions (Gupta and Kumar, 2017; Hussein and Joo, 2019). Siderophores are small organic compounds that contribute to iron chelation and are also assumed to be involved in the mobility of other metals, including zinc (Schalk et al., 2011; Johnstone and Nolan, 2015).

Zinc-solubilizing bacterial inoculants: promising natural biofortifying agents

Improving agricultural production through an eco-friendly approach is paramount in today's world. Numerous strategies are applied for soil nutrient management, including the effects of various chemical fertilizers, leading to decreases in soil fertility, affecting the soil microbial diversity, and posing health-related threats to consumers. Furthermore, various agronomic practices used to increase crop production through a broad range of nutrient intervention strategies are not consumable because such approaches require more time and technical expertise. In addition, the use of environment-friendly fertilizers produced with lower economic inputs could negate the enormous financial burden of costlier chemical fertilizer use. Utilizing zinc-solubilizing bacteria having multiple plant growth-enhancing properties provides a cost-effective strategy for zinc biofortification of various food crops. The addition of zinc to the soil in the form of zinc fertilizers cannot reach the plant system because the transition from the available form of zinc to the unavailable form of zinc prevails in the soil (Upadhayay et al., 2018). Therefore, this problem is solved through the involvement of zinc-solubilizing bacteria, which readily solubilize the inaccessible form of Zn through a variety of mechanisms, including acidification, siderophore production, and production of chelating ligands and oxidoreductive systems (Alexander, 1997; Chang et al., 2005; Saravanan et al., 2007; Saravanan et al., 2011; Upadhayay et al., 2018). Though the secretion of organic acid by zinc-solubilizing bacteria is considered the key mechanism, the well-known organic acids "2-ketogluconic acid" and "gluconic acid" are involved in the process of zinc solubilization (Fasim et al., 2002; Upadhayay et al., 2018). As natural bio-fortifiers, zinc-solubilizing bacteria in the soil provide an accessible form of Zn to plants (Shakeel et al., 2015; Upadhayay et al., 2018; Khan et al., 2019).

The effective colonization of the rhizospheric region by zinc-solubilizing bacteria provides a milieu in which a wide range of metabolic secretions provides valuable means for increased nutrient uptake by plants. There is a wealth of information available on the plant probiotic traits of the zinc-solubilizing bacteria, such as P solubilization, production of ammonia, siderophore, HCN, plant hormones, and exopolysaccharides (Ramesh et al., 2014; Shakeel et al., 2015; Kamran et al., 2017; Upadhayay et al., 2018). A few studies have also shown the role of zinc-solubilizing bacteria in increasing the shoot, root, and overall yield of plants with adequate Zn intake in the edible parts. However, using zinc-solubilizing bacteria (which have extensive plant probiotic properties) as effective bio-inoculants is a relatively newer strategy that offers a long-term solution to the malnutrition problem (Hussain et al., 2018). Zinc-solubilizing bacterial strains such as *Bacillus* sp. (Mumtaz et al., 2017; Javed et al., 2018), *Pseudomonas fragi*, *Pantoea dispersa*, *Pantoea agglomerans*, *Enterobacter cloacae*, *Rhizobium* sp. (Kamran et al., 2017), *Burkholderia*, and *Acinetobacter* (Vaid et al., 2014) have been used successfully as efficient bio-inoculants for executing "bacteria-assisted biofortification". The competent solubilization activity of various Zn compounds such as zinc oxide, zinc carbonate, and zinc phosphate by PGPR has been reported in numerous previous studies (Bhatt and Maheshwari, 2020; Ramesh et al., 2014; Gontia-Mishra et al., 2017; Kamran et al., 2017; Mumtaz et al., 2017; Shaikh and Saraf, 2017; Upadhayay et al., 2022b: Verma et al., 2020).

Lowering the pH of the culture medium also indicates another attribute of zinc-solubilizing behavior of bacteria. Gontia-Mishra et al. (2017) studied the decline in the pH of the culture medium as an important attribute of zinc-solubilizing activity of bacteria and decoded the significance of bacteria in Zn biofortification of rice. Tariq et al. (2007) illustrated the role of zinc-solubilizing inoculants in aborting the zinc deficiency in rice by reporting significant agronomical traits such as increased biomass and grain yield. Zinc-solubilizing bacteria increased the zinc concentration in plants with other growth-related attributes such as increased shoot length and root length and yield maximization (Tariq et al., 2007; Kamran et al., 2017). The importance of zinc-solubilizing bacteria in zinc-deficient soil could be beneficial for better zinc and nutrient transport in plants with little or no involvement of chemical fertilizers. The existence of zinc-solubilizing bacteria in soil, rhizospheric soil, or the presence of ZSB as endophytes makes such agronomically important strains as suitable biofortifying agents. Two bacterial strains, namely, *Azotobacter* and *Azospirillum*, delivered significant and proper Zn content in corn grains (Biari et al., 2008). The pot trial study of Goteti et al. (2013) showed an enhancement in the total dry mass of maize inoculated with *Pseudomonas* and *Bacillus* sp. which resulted in better uptake of Zn, Mn, K, and N. Two endophytic strains (*Sphingomonas* sp. SaMR12 and *Enterobacter* sp., SaCS20) increased the Zn bioavailability in rhizospheric soil and augmented the grain yields with improved zinc densities in the grain part of rice (Wang et al., 2014). Microcosm-based studies revealed the potential candidacy of the *Bacillus aryabhattai* strain as a biofortifying agent as it increased the zinc concentration in edible parts, with an improved yield of soybean and wheat (Ramesh et al., 2014). Other reported strains, including *Pseudomonas fragi* (Kamran et al., 2017), *Exiguobacterium auranticum* (Shaikh and Saraf, 2017), and *B. subtilis* (Moreno-Lora et al., 2019), improved the zinc content in wheat grains. *Providencia* sp. and *Anabaena* sp. improved the nutritional traits of wheat grains in terms of protein content and important micronutrients such as Fe, Cu, Zn, and Mn (Rana et al., 2012). Table 1 displays a summary of recent research on bacterial-assisted improvements in plant growth characteristics and Zn content of edible sections of food-based crops.

ZSB consortia: an auxiliary accomplishment for plant growth and biofortification

The use of a "consortium" consisting of two or more plant growth-promoting bacteria is gaining popularity as a method for encouraging plant development and increasing yield (Menéndez and Paço, 2020). The use of bacterial consortiums has been shown to hasten the growth of plants because the microbial strains contained within the consortium are able to colonize the plant roots effectively. When compared to the use of a single bacterial inoculum, the application of consortia that contain possible strains of PGPR could result in significantly increased plant growth (Backer et al., 2018). "Rhizospheric–endophytic mix inoculants" that had a significant number of "plant probiotic characteristics" increased the plant biomass and sped up the rate at which the plant system absorbed vital micronutrients (Emami et al., 2019). The term "plant probiotic consortia" refers to a group of microorganisms that work together to promote healthy plant growth and reduce the risk of plant death (Zhang et al., 2020). Bacterial consortia have been shown to have beneficial effects on plant life due to the fact that different types of bacteria can work together in a complementary manner to supply mineral nutrients, eliminate inhibitory products, and support one another by virtue of their physical or biochemical properties, all of which have the potential to improve a variety of crucial aspects of the physiology of plants (Molina-Romero et al., 2017).

The primary objective of using ZSB as "bio-inoculants" is to increase the Zn content of the edible parts of plants and, ultimately, increase crop yield. However, the role of ZSB consortium in Zn biofortification has not been thoroughly investigated. The concept of "microbial-assisted biofortification approach" can be further decoded using a modest number of research studies available on the ZSB-based consortium. Exploration, formulation, and development of successful bacterial consortia is a crucial research topic with the potential for sustainable biofertilizer applications in agriculture (Menéndez and Paço, 2020). A rhizobacterial consortium of three strains (one of *Burkholderia* and two of *Acinetobacter*) was found to increase the Zn levels and its uptake in wheat straw and grain (Vaid et al., 2019). The application of a beneficial bacterial consortium (*E. cloacae* and *Bacillus megaterium*) and fertilizers labeled as "zinc sulphate" resulted in the highest level of soil exchangeable zinc, increased Zn uptake in grain parts, and increased grain yield (Rezaeiniko et al., 2019). Inoculation with a consortium (*Pseudomonas* sp. and *Rhizobium leguminosarum*-pr-1) increased the Zn levels in plant shoots (Mishra et al., 2012). One consortium of two zinc-solubilizing *Bacillus* species (*Bacillus* sp. SH-10 and *B. cereus* SH-17) was assessed as an efficient biofortifying agent to generate rice crops enriched with Zn in grains and exerted the highest "zinc translocation index" from 1.6 to 1.7 (Shakeel et al., 2015). The treatment combining a consortium of *Burkholderia cepacia* and *Pantoea rodasii* with ZnO supplement had the highest Zn concentration in rice grain (25.07 mg/kg) compared to the control (15.80 mg/kg) (Upadhayay et al., 2022b). 'PD16' and 'NDR359', two subsequent rice cultivars subjected to treatment by the ZSB consortium (*Burkholderia* and *Acinetobacter*, respectively), had the highest Zn levels in grains, *i.e.*, 16.1 mg/kg (in 'PD16') and 16.0 mg/kg (in 'NDR359') (Vaid et al., 2014). During the field trials, two consortia of *A. lipoferum* (JCM-1270, ER-20) and *Pseudomonas* sp. (K-1, 96-51), as well as a single strain of *Agrobacterium* sp. (Ca-18), demonstrated positive results in zinc biofortification of rice grains with improved growth, physiology, and yield of rice plants (Hafeez et al., 2002; Tariq et al., 2007; Hussain et al., 2018). Blue-green algae were also studied for their role in elemental biofortification. The consortium of *Anabaena* sp. (CR1) and *Providencia* sp. (PR3) with 75% RDF and zinc increased the Zn uptake (323.8 g/h) in the wheat crop (Shahane et al., 2017). Kumar et al. (2017) investigated the effect of co-inoculation of *Enterobacter* and *Serratia marcescens* on better micronutrient uptake by wheat, finding that this consortium-based bio-inoculant boosted the Zn content by 32% in the pot trial and 23% in the field study. As a "possible Zn solubilizer", the PGPR consortium (*Pseudomonas* sp. and other PGPR strains) boosted the Zn content of rice by up to 157% (Tariq et al., 2007). The *Anabaena–Azotobacter* biofilm consortium boosted zinc accumulation (107.01 µg g^{-1}) in maize flag leaf, demonstrating cyanobacterial-mediated Zn biofortification (Prasanna et al., 2015).

Concept of bioeconomy: A new way of green economy

"Bioeconomy" is considered an important means to tackle emerging global issues, including climate change, food insecurity, and a massive reliance on manufactured sources (Ollikainen, 2014; Uzoh and Babalola, 2018). Many authors gave various definitions of the bioeconomy and provided a conceptualized view of the bioeconomy for sustainable development. Nevertheless, according to the European Commission (2012), "bioeconomy" is illustrated as an economy that uses plant and animal residues and the wastes they produce from land and water bodies (as raw materials) for industry and fulfills the purpose of generating electricity. In contrast, the OECD defines bioeconomy as "economic outcomes derived from biotechnology" (OECD, 2009). Furthermore, in the Indian context, the concept of bioeconomy is linked to the biotechnology industry (Rengalakshmi et al., 2018). The "bioeconomy" harnesses new knowledge from agricultural science research to produce a variety of crop-derived products, and it is an important component of long-term agricultural development. To accomplish the task of developing a robust bioeconomy, research in agricultural and resource economics becomes necessary to develop robust policies to guide the progress of the bioeconomy (Zilberman et al., 2018). The concept of "bioeconomy" through a mission called "National Mission on Bioeconomy" has gained prominence and has become a sole concept in South Asian countries like India to promote bioresources in a sustainable agricultural system (Rengalakshmi et al., 2018).

The unique initiatives of the Indian government, such as "Make in India" (launched in 2014), also include the bioeconomy as a main component (Biotechnology Industry Research Assistance Council (BIRAC), 2016; Rengalakshmi et al., 2018). The bioeconomy has three crucial and essential elements, such as (a) advanced developments in gene and cellular science to develop novel products, (b) use of renewable biomass or use of bioprocesses for sustainable production, and (c) integration of biotechnological knowledge to investigate novel products (McCormick and Kautto, 2013; Leitão, 2016). Here biomass is any substance of biological origin, such as an entire or precise part of animals, plants, trees, marine organisms, and microorganisms (Leitão, 2016). The agricultural system is the lifeline of humanity as it provides a continuous supply of food, fuel, and fiber, thus incorporating value-added products to build an efficient bioeconomy. The agroecosystem is seen as an essential element in maintaining the balance and different interactions between different components of the environment (Rengalakshmi et al., 2018). An efficient bioeconomy can be built by producing microbe-based products such as biofertilizers for sustainable and increased production of crops from less available resources (Uzoh and Babalola, 2018). The important approach of the bioeconomy in sustainable agriculture is to improve the biological properties of soil and reduce the pessimistic impact of the soil on the local environment (Rengalakshmi et al., 2018). Accordingly, bio-inoculants, which can increase plant growth, have been used as natural resources to enhance crop productivity. PGPR are also known as "biostimulants" and may be used as biofertilizers to boost the bioeconomy through sustainable agricultural production. Bacteria with zinc-solubilizing traits are employed as effective bio-inoculants to maintain the proper micronutrient concentration in the edible section of crop plants, offering biofortification benefits to food-based crops (Upadhayay et al., 2018; Upadhayay et al., 2019; Upadhayay et al., 2022a; Upadhayay et al., 2022b). These kinds of bioresources could be very helpful for food security by making crops grow better and reducing the need for artificial fertilizers.

The bioeconomy is broadly understood in biofuel production, but the role of agriculture in empowering the bioeconomy cannot be ignored. From the perspective of agriculture, the bioeconomy describes continuous and sustainable agricultural production through bioresources. The bioeconomy uses the facts or wisdom of innovation in life sciences and biotechnology, involving technologies to develop and establish eco-friendly bioeconomy-based practices and products. This zinc-solubilizing bacterial approach is described in this manuscript as an eco-friendly strategy for enhancing plant growth and fortifying plants with zinc. In this way, synthetic fertilizer use will be minimized, and microbe-assisted crop output will be improved.

The following concepts for developing a greener economic approach should be considered:

1. Using the organic farming approach to curb the high demand for chemical fertilizers.
2. Using bacteria that dissolve zinc and other biostimulants as natural bioresources to prevent zinc malnutrition.
3. Reducing the use of chemical fertilizers to reduce the negative impacts on the environment is a way to go.
4. Promotion of research into the functional use of agriculturally important microorganisms in sustainable agricultural production in order to reduce the use of chemical or synthetic fertilizers or pesticides.

A more eco-friendly use of natural bio-resources in the economy, especially in agricultural production, can create a

TABLE 1 Impact of zinc-solubilizing bacteria on crop growth attributes and zinc biofortification benefits.

Zinc-solubilizing bacteria	Crop	Growth attributes	Edible part	Amount of Zn in edible part	References
Bacillus cereus ZnSB13	Chickpea (*Cicer arietinum* L.)	Increment in fresh and dry nodule weights, shoot and root dry weight, effective grain yield	Grain	38%	Batool et al., 2021
Pseudomonas spp., VBZ4	Tomato (*Solanum lycopersicum* L.)	Taller plants, broader stems, higher fresh and dry shoot and root weights, and a greater number of fruits per plant	Fruit	2.87 mg/100 g	Karnwal, 2021
B. aryabhattai ZM31 + *B. subtilis* ZM63	Maize (*Zea mays*)	Maximum cob length and cob dry weight, maximum stover and grain yield	Grain	52.0 mg kg^{-1}	Mumtaz et al., 2020
B. subtilis QST713	Wheat (*Triticum durum* cv Amilcar)	With the rock phosphate supply, the bacterial inoculant increased the root dry mass and total dry mass	Grain	41 mg/kg	Moreno-Lora et al., 2019
R. tropici + *B. subtilis*	Common bean (*Phaseolus vulgaris* L.)	Improvement in shoot dry matter and grain yield	Grain	307 g/ha	Jalal et al., 2021
B. aryabhattai MDSR14	Soybean	Increased plant height and increase in root and shoot dry weight	Grain	82.20 μg g^{-1}	Ramesh et al., 2014
B. tequilensis CRS-38 + Zn3 $(PO_4)_2$	Wheat	Enhancement in length and dry weight of both root and shoot	Grain	(53.25 μg g^{-1}	Yadav et al., 2022
Exiguobacterium aurantiacum MS-ZT10	*Triticum aestivum*	Increment in shoot and root length, chlorophyll content, dry weight	Grain	18.2 ppm	Shaikh and Saraf, 2017
Burkholderia cepacia (BMRR126) + ZnO	Rice	Increment in plant height, number of tillers per hill, dry matter accumulation, and improved grain yield	Grain	33.25 mg/kg	Uadhayay et al., 2022b
Bacillus altitudinis SRI-178	Chickpea	Significant enhancement in shoot height and root length, improvement in grain yield	Grain	4.5 mg/100 g	Gopalakrishnan et al., 2016
Pseudomonas plecoglossicida SRI-156, *Brevibacterium antiquum* SRI-158	Pigeonpea	Significant enhancement in shoot height and root length, improvement in grain yield	Grain	4.0 mg/100 g	Gopalakrishnan et al., 2016

new "green economy" sector. Harmful environmental side effects associated with intensive agricultural practices have led to the rise of sustainable agricultural production options (Scialabba and Hattam, 2002; IFOAM, 2005; Rengalakshmi et al., 2018). Examples of such options are organic farming, natural farming, sustainable farming with low external inputs, and zero-budget farming (Rengalakshmi et al., 2018). Among these possibilities for sustainable agricultural production, "organic farming" is a widely adopted method that excludes the use of synthetic fertilizers. The demand for organic farming has increased worldwide, as it is more eco-friendly than conventional farming (Darnhofer et al., 2010; Eyhorn et al., 2019). Organic farming yields are lower than those of conventional farming, but it is notable for producing more nutritious foods with fewer pesticide residues in a more profitable and eco-friendly manner (Ponisio et al., 2015; Smith et al., 2019). Organic farm soils have more organic carbon, enzymatic activity (dehydrogenase and alkaline phosphatase), and microbial biomass than in conventional farms (Melero et al., 2006; Ramesh et al., 2010). Compost, manure, additives, and crop wastes change the soil microbial biomass and, along with bio-inoculants, are essential for plant vitalization.

Biofertilizers and biopesticides have received much attention in the bioeconomy to increase soil fertility and crop productivity while maintaining environmental sustainability (Truu et al., 2008; Rengalakshmi et al., 2018). These two bioeconomy-based products (bio-fertilizers and bio-pesticides) are considered safe to use and provide a suitable food and nutrition security option.

Employing bio-based stimulants in sustainable agriculture

Biostimulants are microorganisms prescribed to agriculture as bio-inoculants (biofertilizers) to address global issues in a sustainable way. These issues include the use of chemical fertilizers or agrochemicals, strict farming techniques, and environmental factors like global warming and climate change. Therefore, innovation is needed to manage sustainable agricultural output without negative environmental repercussions (Milder et al., 2015). Literatures show the significance of microorganisms in agriculture through the creation of bio-inoculants and their effects on agricultural production. Researchers worldwide are using bio-inoculants to improve the economic situation of farmers with microbe-based natural fertilizers. Microorganisms promote crop growth by solubilizing substances (phosphorus, iron, and zinc), fixing N_2, and secreting enzymes (like indole acetic acids) (Ahemad and Kibret, 2014). Several plant growth-promoting properties of bio-inoculants provided hope for future generations to produce healthy and nutritious crop-based foods with less expensive inputs.

Exploiting bio-inoculants for sustainable agriculture production strategies should contain the following key attributes:

- Exploration of plant growth-promoting microorganisms from a diverse range of soils.
- Analysis of desirable attributes in isolated microorganisms and their use as suitable bio-inoculants for plant growth-enhancing properties for various food crops.
- Bio-inoculants must have positive impacts on soil health, soil nutrients, and crop yield maximization.
- Formulation and preservation of efficient bio-inoculants.
- Promoting organic farming through the use of "bio-inoculants" over more expensive agrochemicals.
- Popularizing the use of bio-inoculants/biofertilizers/biopesticides among farmers.
- Minimizing environmental damage from chemical fertilizers.

Zinc-solubilizing bacteria in the context of the green economy

Zinc scarcity in soils affects crops, resulting in low zinc levels in the edible parts of crops. Other problems of low soil fertility arise from the rigorous exploitation of chemicals (agrochemicals, especially pesticides, fungicides, herbicides, insecticides, *etc.*). Hence, the world is looking for a greener farming approach where farmers can grow high-quality cash crops without chemicals. Most companies around the world manufacture fertilizers and other chemicals that are recommended for various crops. However, the high fertilizer prices make it impossible for many farmers to buy fertilizer and apply it efficiently to the field to improve crop yields. The argument over the intensive use of agrochemicals will not be fruitful until we encourage green agriculture among farmers. It is clear proof that applying chemical-based fertilizers brings higher crop yields and economic empowerment to farmers. On the other hand, it causes problems in the environment, such as loss of soil fertility, and health problems for people. Zinc shortage affects crop yields and leads to the development of Zn-deficient crops; hence, the majority of the world's population may be deprived of enough zinc if they rely on these crops for their primary source of nutrition (Khan et al., 2009; Upadhayay et al., 2018). The zinc-deficient soils also impede crop growth and overall productivity (Kamran et al., 2017), leading to large economic losses for farmers due to the unprofitable selling of low-quality grains in the market. There is also a need to give stable, nutrient-rich, crop-based foods to a large part of the population who are malnourished because of the lack of micronutrients.

Therefore, an organic farming practice can overcome this problem, and zinc-solubilizing bio-inoculants can replace the intensive fertilizer application. The use of zinc-solubilizing bacterial inoculation is a green technology to improve crop quality; thus, as a natural biofortifying agent, it will play a key role in the future by alleviating Zn-associated malnutrition in humans through the intake of foods from the biofortified crop (Upadhayay et al., 2018; Khan et al., 2019; Upadhayay et al., 2019). This strategy would be helpful in most regions of the world where diverse foods are not accessible to the local human population and most people cannot afford dietary supplements (Hussain et al., 2018). Both bacteria and fungi have been explored to enhance Zn accessibility in the rhizospheric region and improve Zn concentration in the comestible parts of crops (Subramanian et al., 2009). Several previous reports documented that the application of zinc-solubilizing bacteria for agriculture production could open a new door to strengthen the bioeconomy. Figure 1 depicts the application and commercialization of zinc-solubilizing microorganisms as an emergent green approach to further cultivate the concept of bioeconomy for the well-being of local farmers.

Conclusion

Improving zinc content in crops is the prime need of a large section of the world population suffering from zinc malnutrition through a microbe-assisted zinc biofortification approach. The next goal is to launch several crop improvement programs to develop a strong bioeconomy in a more sustainable manner without reliance on chemical fertilization. Microbial bio-inoculants in the form of zinc-solubilizing bacteria solve this purpose by providing benefits to consumers by increasing the biomass and grain yield and biofortification benefits by increasing the appropriate zinc level in the edible portions of plants. Zinc-solubilizing bacteria in soil solubilize insoluble zinc into a soluble form; since they have the traits of plant growth-promoting activities, they also serve as crop-vitalizing agents. Increased crop production in response to zinc-solubilizing bacteria can meet the bioeconomy goals, such as (a) food security for the escalating world population, (b) plummeting reliance on non-renewable resources for crop production, such as the intensive use of fertilizers and rigorous agricultural practices, and (c) use of ZSB for enhanced crop production in a more sustainable manner without showing the negative impact on the environment. Future research aims to understand the zinc-solubilizing microbial diversity and the site-specific rhizomicrobiome with deep insights into zinc-solubilizing mechanisms. Further innovations require the development of "engineered zinc-solubilizing bacteria" with massive plant growth-promoting properties through genetic modifications

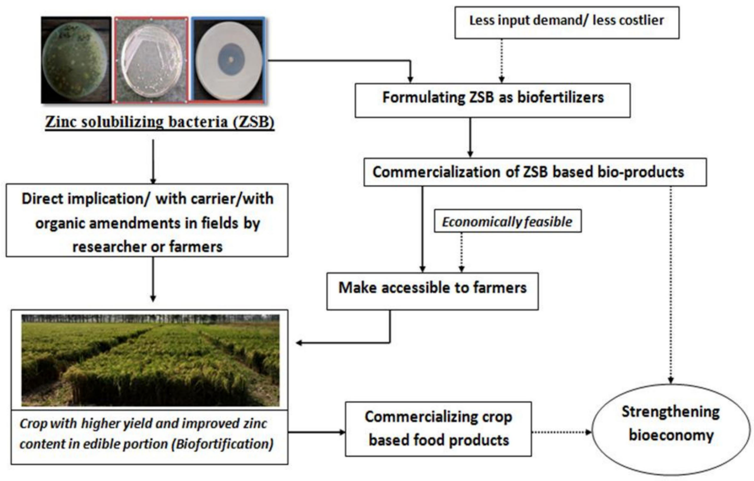

FIGURE 1
Overview of zinc-solubilizing bacteria (ZSB) formulation and commercialization of microbe-based products for crop growth and zinc biofortification of edible parts. The formulation of ZSB is an environment-friendly approach with less input and provides cost benefits to farmers. The commercialization of biofortified crop products along with ZSB-based biofertilizers can improve the green economy (bioeconomy).

and their commercialization for sustainable crop production. In short, using bioresources in the form of zinc-solubilizing bacteria is expected to improve the quality and productivity of crops with Zn biofortification benefits and consequently enhance the green bioeconomy.

Author contributions

VKU: writing of the original draft of the manuscript. AVS: conceptualization and editing. AK and AS helped in writing and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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