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Plant-Microbe Interaction in Improving Zinc Nutrition in Rice: A Review

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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Review Article

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ABSTRACT

Zinc is an essential micro-nutrient that affects metabolic activities, including growth and cell proliferation in all living organisms. Zinc deficiency in agricultural soil has been increasing at an accelerated rate all over the world, leading to its deficiency in plants as well as humans. Zinc solubilising bacteria (ZSB) solubilise complex zinc in soil into plant absorbable compounds through several mechanisms such as the production of acid, chelating compounds, protons etc. further improving its bioavailability in plants and humans. Improving zinc nutrition through microbes is an effective measure to overcome its deficiency. ZSB with Plant Growth Promoting (PGP) traits can be an additional advantage as along with increasing zinc amount in plant it would also promote overall growth of plants through PGP traits and can act as a biocontrol agent against several crop

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pathogens. In this review we attempt to study the significance of zinc; status and deficiency of zinc in Indian soil and to understand how zinc solubilizing bacteria can prove to be an effective measure to increase zinc content in plants and overcome its deficiency.

Keywords: Zinc; rhizosphere; deficiency of Zn; zinc solubilising bacteria; soil bacteria; plant growth promoting rhizobacteria; Zn nutrition.

1. INTRODUCTION

Zinc is an essential micronutrient for all living things. It is an essential component of several enzymes that are required for the synthesis, degradation, and metabolism of lipids, proteins, nucleic acids, carbohydrates, and other micronutrients. The molecular structure of cellular components must be preserved by zinc in order to maintain the integrity of cells and organs [1]. Deficiency of zinc affects metabolic activities, including growth and cell proliferation in plants, humans and microorganisms [2]. Zn deficiency prevails among approximately 2 billion people in the world causing growth retardation, an impaired immune system, hair loss, diarrhoea and delayed sexual maturation. Plants uptake zinc from the soil and subsequently, it moves up the food chain to humans. Prevalialence of zinc in soil is in the form of augite, biotite, hornblende, olivine, and sphalerite ores. Zinc deficiency in agricultural soil accounts for 49% of the global scale and in India, 48-50 % of such soil is deficient in zinc. This decline in soil micronutrients leads to low yield of crops including rice and also causes deficiency in human population causing several diseases. Rice being a staple food, consumed by maximum population, increasing its zinc content by fortification can be a step to overcome zinc deficiency in humans. In India, low Zn soils often cause insufficient intake of Zn in the human population causing its deficiency. In Odisha, rice variety Swarna is widely cultivated, which is also deficient in Zinc [3].

Despite the fact that the soil contains more than enough zinc to sustain crop growth, plants are unable to absorb it because of inaccessible zinc fragments. The availability of zinc in the soil is influenced by a wide range of factors, such as soil phosphorus, pH, texture, and weather. Since zinc quickly transforms into inaccessible components and accumulates in the soil, exogenous zinc use in fertilisers is also unconventional. The anticipated global population in 2050 will reach 9.7 billion people (approx.). India population is expected to increase by addition of 273 million by 2050 [4]. With the application of chemical fertiliser applications and many breeding procedures to boost the Zn content in cereal grains, researchers are looking at several strategies to reduce Zn insufficiency among human populations [5]. Zinc is supplemented to the soil through expensive chemical fertilizers in the form of Zn-Sulphate or Zn-EDTA which changes to insoluble complex structures within 7 days of application and cause environmental hazard [6]. Hence, an effective and inexpensive alternative to the chemical application is the use of Zinc Solubilizing Bacteria (ZSB).

Several methods have been employed recently to lessen host plant zinc deficiencies. Among these, applying chemical fertilisers is an expensive and unsustainable method that increases crop susceptibility to diseases and gradually lowers soil fertility. Furthermore, careless fertiliser application has contaminated the water and soil, posing a risk to plant life as well as human health. As a result, scientists are particularly interested in using affordable, environmentally friendly methods to increase nutrient availability (particularly zinc) without compromising the environment [7]. ZSB readily solubilise complex zinc present in soil into soluble compound improving its bioavailability and uptake by the crop plants, subsequently entering to human through the food [8]. Zinc solubilising bacteria solubilise complex zinc by mechanisms like acidification [9], production of siderophores [8] and proton, oxidoreductive systems on cell membranes. Biofortification of Zinc through microbes is an effective measure to overcome its deficiency [10]. ZSB with Plant Growth Promoting traits can be of additional advantage which cannot only increase availability of Zn and other elements in soil but also can enhance growth of plants through PGP traits and can perform as a biocontrol agent against several crop pathogens [11].

Therefore, an attempt has been made to review the significance of zinc; status and deficiency of zinc in Indian soil and to understand how zinc solubilizing bacteria can effectively increase zinc content in crops and overcome its deficiency.

2. SIGNIFICANCE OF ZINC

2.1 Plants

Zinc (Zn), an essential micronutrient, is required for healthy plant, animal, human, and microbial growth and development. It is essential for protein synthesis, glucose metabolism, enzyme activation and activities in general [12]. Zinc has a critical function in plant physiology, particularly in photosynthesis, chlorophyll synthesis, nitrogen metabolism, and stress resistance in plants. It is necessary for the development of optimal fruit size and high crop yields [13,14]. Zn is required for auxin synthesis in plants. Basically, auxin governs the process of cell division and elongation, hence in Zn deficit conditions, stunted growth, small & distorted leaves, reduced pollen production and internode restrictions are seen [15]. Moreover, zinc plays a significant role in transcription factors needed for cell differentiation and proliferation [16]. Zinc is primarily known to inhibit enzyme activities as an antioxidant and to cause high levels of oxidative stress, which may be the cause of the chloroplasts' deformation [17]. Reduced leaf photosynthetic ability as a result of such photosynthetic centre death makes leaves more vulnerable to photodegradation [18].

2.2 Animals and Human Beings

All living organisms' cellular processes depend critically on zinc, which also helps human's immune systems. Several body enzymes have zinc as a catalytic and structural component. Zinc deficiency in the body can cause a variety of health issues, such as weakened body muscles, a compromised immune system, problems with learning and physical development, memory loss, hair loss, and skin problems. Inadequate levels of Zn also lead to DNA damage and can aggravate the risk of cancer [19]. Infertility is a common threat that has been observed with zinc deficient male population. In case of pregnancy, reduced Zn intake results in stunted brain development of the fetus and also congenital diseases like acrodermatitis enteropathica [20-24,12].

2.3 Microbes

Zinc plays a significant role in the regulation of microbial virulence and host immune responses.Deficiency of zinc levels in microbes can cause imbalance in zinc homeostasis and disregulation of intracellular signalling pathways. Additionally zinc acts as a cofacter for several bacterial proteins such as DNA replication and protein synthesis, hence it is required for enzymatic reactions, responses to oxidative stress situations, DNA repair and regulatory roles in various physiological processes in bacteria [25].

3. DEMAND AND SUPPLY OF ZINC

Soil is the primary source of Zinc to plants whereas animals including humans obtain it through the food chain. Ideally, the Zinc concentration of healthy and productive soil should be 10–300 mg/kg [26]. However, it is the most deficient micronutrient in the soil and according to estimates, the zinc content of 49% of the world's agricultural soils is insufficient. About 50% of agricultural soil in India is affected with Zn deficiency, which ranges between 30-72 mg/kg and hence, responsible for nearly 40% reduction in productivity [27]. Zinc content is considerably high, mostly present in mineral forms like smithsonite (ZnCO3), Zincite (ZnO), Sphalerite (ZnS) and several other ferrous and silicon mineral forms but it is insoluble and unavailable for plant uptake leading to its deficiency [21]. Optimal zinc concentration required for plants ranges between 20-100 mg/kg. Since the soluble zinc content is low in soil, deficiency of zinc in plants has also been observed.

Low Zn soils in India often result in inadequate Zn intake in the population, which causes a deficiency. Furthermore, one third of the world's population affected with zinc deficiency. Considering that human body is unable to store zinc, it has to be consumed from zinc enriched food sources. For an adult human, the optimal dietary requirement of zinc is 15mg per day [12] necessary component for several zinc binding proteins and nucleic acid. Meat products like beef, pork, chicken and breakfast cereals such as oats, almond, peanut, walnut etc. and yogurt, cheese, milk and other dairy products are known to be rich in Zinc content [28-31]. Reduced cellular immunity and a later antibody response can result from insufficient Zn absorption and uptake [32] hence, it is required to be taken up by human body in adequate amount. In case of animals, zinc supplements are found to be efficient for cattle to accelerate recovery in case of bovine rhinotracheitis [33]. Zn deficiency causes several viral infections in animals. Even though it is required in a less amount zinc is truly indispensable by all living forms.

4. CAUSE OF ZINC DEFICIENCY IN SOIL

In soil zinc is mainly present in complex insoluble form that is unavailable to plant. Worldwide, zinc concentration of soil ranges approximately between 2-25 ppm of which a large proportion is trapped in iron and manganese oxides and other insoluble forms [34] leading to zinc deficiency and significantly affecting the crop yield. There are several factors that give rise to zinc deficiency in soil. Soil texture for instance; scalped and sandy soils are more prone to zinc deficiency than well managed soils such as silty or clayey soil. Besides, severe soil compaction leads to zinc deficit conditions. In addition to soil texture; pH, phosphorous and Iron content and weather conditions influences the zinc content of the soil. Solubility of zinc is mostly influenced by the pH of the soil; hence, alkaline conditions reduce zinc's solubility and availability. Consequently, zinc deficiency widely prevails in soil with pH above 6.5 [35]. Along with pH, zinc deficiency appears more in flooded soil and wet weather as compared to sunny weather [36,34]. Hence water content of the soil is an important determinant for bioavailability of zinc [37]. Furthermore, overuse of Phosphorous fertilizers may lead to zinc deficiency in some cases as phosphorous precipitates zinc in soil or at root soil interface and intervene with zinc metabolism inside the plant cells [34]. High concentration of Iron has also found to decrease the bioavalability of Zinc under anaerobic condition [38]. Therefore, in order to enhance the bioavailability of Zn, use of organic matter could be taken into account [39].

Insufficient amount of Zinc in soil severely affects the quality of production and yield of crops. It was opined by several researchers that 15-60 ppm of Zn supply is necessary for proper metabolic functioning of plant tissue and crop plant [40,41]. In agricultural practices expensive chemicals in form of Zn-Sulphate and Zn-EDTA are applied to the soil to supplement zinc. Nevertheless, these chemical inputs subsequently change into insoluble complex structures within 7 days of application and cause environmental hazard [6]. Besides, these fertilizers are expensive and unaffordable by the farmers. Hence, an organic, environment friendly substitute to the chemical approach is the application of Zinc Solubilizing Bacteria (ZSB) which readily solubilises complex Zinc present in soil into a soluble compound increasing its availability to plants.

5. ZINC SOLUBILIZING BACTERIA (ZSB)

A particular group of microorganisms can be used to convert the soil insoluble zinc into soluble form can overcome zinc deficiency achieving the objective of nutrient management and sustainable agriculture [42]. ZSB are the rhizospheric bacteria which can be used in the form of bio-inoculants to increase availability of native zinc for crop assimilation. Several bacterial and fungal strains are known to solubilise zinc. Some zinc solubilising bacteria are species of *Bacillus*, *Gluconacetobacter*, *Azotobacter*, *Azospirillum*, *Thiobacillus ferrooxidans, Thiobacillus thiooxidans*, *Acinetobacter, Cyanobacteria, Serratia, Pseudomonas* and facultative thermophilic iron oxidizers [43-45]. (Table.1). In case of fungal strains, arbuscular mycorrhizae and *Trichoderma* are known to exhibit zinc solubilising traits [46]. *Bacillus* sp. are given special interest as they are spore-forming, hence they can sustain in adverse stress conditions, and can be mass cultured into easy formulation and also known to form non-specific association with several host crops [47-49]. Bacteria immobilize zinc metal by the process of precipitation and adsorption. As zinc is a limiting factor in crop productivity, zinc solubilization by bacteria plays an important role in zinc nutrition to plants [45].

Although adopting suitable crop rotation can prove to be a positive agronomy approach for improving Zn phytoavailability, application of beneficial zinc solubilising rhizospheric microbes as bio-inoculants to increase tissue zinc concentration in plants and crops can be advocated to be a long-term cost-effective solution to attain sustainable agriculture [48] and to eliminate the zinc malnutrition in humans [80]. Therefore, utilization of zinc solubilising and mineralizing bacteria could be a relevant solution to zinc deficiency in crops and human.

6. MECHANISMS OF ZSB

Zinc solubizing bacteria solubilise complex zinc through various mechanisms like production of chelating ligands, amino acids, vitamins, phytohormones, siderophores, acidification, oxido-reductive systems on the cell membrane and proton extrusion [81]; [9]; [63]. Some of the basic mechanisms exhibited by ZSBs for zinc solubilisation are:

6.1 Acidification

Among all, the secretion of organic acids is a major zinc solubilizing process ZSB release organic acids in the soil that sequester Zinc cations while simultaneously decreasing the pH of the neighbouring soil and making it available to plants, increasing Zn content [9]. Amongst all the organic acids, 2-ketogluconic acid and gluconic acid produced by the isolates, results in solubilisation of zinc. However, the organic acid secretion by microbes varies depending upon the substrate of Zn minerals. It is also reported that some species of ZSB produce several organic acids such as oxalic, lactic, citric, malic, glycolic, malonic, tartaric, formic and succinic acids to solubilise zinc [82-84]. Additionally, a change in pH with inoculation of *Pseudomonas* spp. and *Bacillus* spp. in broth culture indicate solubilisation of ZnS, ZnO and $ZnCO_3$ [81]. Furthermore, the acid production tends to vary with respect to the Zn substrate provided in the media [84]. Several reports have suggested that ericoid and arbuscular mycorrhizal fungi lower the pH of rhizospheric soil by producing organic acids that solubilise complex zinc [56,85]. *Bacillus* sp. AZ6 was able to readily solubilize complex metals by secreting cinnamic, caffeic, chlorogenic, syringic, ferulic and gallic acid in a liquid medium [44].

6.2 Chelating Ligands

There are specific and non-specific transporters involved in essential metal ions uptake across the cytoplasmic membrane of bacteria driven by a chemiosmotic gradient [86]. Zinc is a highly reactive metal that is less persistent in soil which leads to its deficiency in plant. Zinc bioavailability can be enhanced with help of Zn chelating compounds [87]. The rhizospheric microflora is known to release Zn chelating compounds that increase its availability to plant roots. Reports suggest that production of Zn chelating metallophores by *Pseudomonas monteilii*, *Microbacterium saperdae* and *Enterobacter cancerogenus* helps in generation of soluble zinc molecules in soil for plant uptake [88]. Another report suggested that biofertilizer consortia of *Pseudomonas* sp. (96-51), *Azospirillum lipoferum* (JCM-1270, ER-20) and *Agrobacterium* sp. (Ca-18) produced ethylene diamine tetra acetic acid as a chelator that attached to Zn and increases its availability for plant uptake [89].

6.3 Alteration in Root Structure

Reports also indicate that change in root structures affects the availability of soluble zinc. Increase in surface area and root growth can lead to maximum uptake of Zn [85]. For instance, mycorrhizal fungus tends to increase the surface area of the roots that results in increased uptake of nutrients including zinc by plants. Arbuscular mychrohhizae are able to acquire zinc from 40mm distance of root surface [90]. With inoculation of potent ZSBs, there was accelerated growth in root weight, length, volume and zinc content of rice [89].

6.4 Others

In some cases, cell wall modification and bio-precipitation has also been reported [91]. *Gluconacetobacter diazotrophicus* PA15 was able to solubilize ZnO by producing sugar such as glucose or sucrose as the potent carbon source [43]. *Several Bacillus* strains are known to readily solubilizes complex Zn through production of plant hormones, amino acids, proton extrusion and oxido-reductive systems of the cell membranes [92].

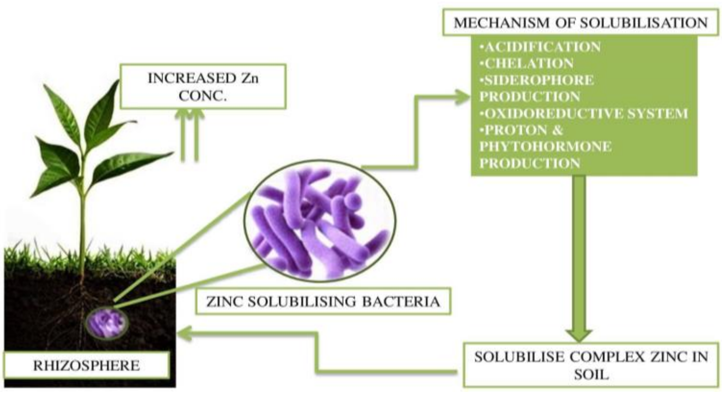

Fig. 1. Zinc solubilising bacteria mechanisms

Table 1. Some effective zinc solubilizers isolated and characterized

Microorganisms known to solubilise zinc	Source of organism	Source of Zinc	References
Aspergillus niger A. omius A. oryzae	-	ZnO, $Zn_3(PO_4)_2$	[50]
Penicillium luteum	soil	ZnO, $Zn_3(PO_4)_2$	[51]
Pseudomonas fluorescence	forrest soil	$Zn_3(PO_4)_2$	[52]
Trichoderma harzianum Rifai	soil	Granular metallic Zn	[53]
Pseudomonas aeruginosa	Airborne bacteria isolated from a tannery air environment	ZnO and $Zn_3(PO_4)_2$	[54]
Bacillus sp. and *Pseudomonas* sp.	zinc ore sphalerite; paddy soil	ZnO, ZnS and $ZnCO_3$.	[55]
Hymenoscyphus ericae and *Oidiodendron maius*) (Ericoid mychorrhizae)	Heavy metal polluted sites	ZnO, $Zn_3(PO_4)_2$	[56]
Beauveria caledonica	Unpolluted soil, lawn, UK	$Zn_3(PO_4)_2$	[57]
Gluconacetobacter diazotrophicus	Rot tissue of carrot, raddish, beetroot and coffee	ZnO $ZnCO_3$ or $Zn_3(PO_4)_2$	[58,43]
Klebsiella sp. *Pseudomonas* sp.	Soybean and Mung bean rhizosphere	ZnO, $Zn_3(PO_4)_2$	[21]
Burkholderia sp., *Acinetobacter* sp. and *Acinetobacter* sp.	soil	DTPA	[59]
A. terreus (ZSF-9)	Agricultural field soils	ZnO, $ZnCO_3$, $Zn_3(PO_4)_2$	[60]
Enterobacter cloacae	Rice rhizosphere	ZnO, $ZnCO_3$, $Zn_3(PO_4)_2$	[10]
Bacillus cereus	Zn deficit soil	ZnO, $Zn_3(PO_4)_2$	[61]
Ralstonia picketti, Burkholderia cepacia, and *Klebsiella pneumoniae*	Zinc fertilizer rich rice rhizosphere	ZnO , $ZnCO_3$	[62]
Bacillus sp., *Bacillus aryabhattai* , *Bacillus subtilis* and *Bacillus aryabhattai*	Maize Rhizosphere	ZnO	[63]
Pseudomonas fragi , *Pantoea dispersa* and *Pantoea agglomerans*	soil	$ZnCO_3$	[9]
Acinetobacter sp., *Serratia* sp.	Rice soil, Malaysia	ZnO $ZnSO_4$	[64]
B. aryabhattai, Pseudomonas taiwenensis	Stone quarry Dust Powder	ZnO, $Zn_3(PO_4)_2$, $ZnCO_3$	[65]
B. megaterium	Rhizosphere of wild pepper	ZnO, $Zn_3(PO_4)_2$ $ZnCO_3$	[66]
Agrobacterium tumefaciens and *Rhizobium* sp.	Rhizosphere of barley and tomato	ZnO, $Zn_3(PO_4)_2$, $ZnCO_3$	[67]
Pseudomonas sp. and *Bacillus* sp.	Chickpea Rhizospheric	($Zn_3(PO_4)_2.4H_2O$	[68]
Bacillus megaterium	Cow dung	ZnO , $ZnCO_3$	[69]
Sphingobacterium multivorum, Burkholderia cenocepacia, Bacillus xiamenensis, Burkholderia ambifaria, and *Bacillus aerius*	Mycorrhizal corn roots	ZnO, $ZnCO_3$	[70]

Microorganisms known to solubilise zinc	Source of organism	Source of Zinc	References
Acinetobacter baumannii; *Burkholderia cepacia*	-	ZnO, $Zn_3(PO_4)_2$, $ZnSO_4.7H_2O$	[71]
Burkholderia vietnamiensis and *Burkholderia seminalis*	Rice rhizosphere	$Zn_3(PO_4)_2$ and $ZnCO_3$	[72]
Pseudomonas frederiksbergensis	Jujube rhizosphere	ZnO, $Zn_3(PO_4)_2$	[73]
Serratia sp., Acenitobacter sp.	Wetland Rice field	ZnO, $Zn_3(PO_4)_2$, $ZnCO_3$	[74]
Pseudomonas aeruginosa, Pseudomonas taiwanensis and *Beijerinckia fluminensis*	Rhizospheric region	ZnO, $Zn_3(PO_4)_2$, $ZnCO_3$	[75]
Bacillus sp. & Enterobacter sp.	Root nodules of wild legumes	$ZnCl_2$ (0.2-1.0 g conc.)	[76]
Priestia megaterium, Priestia aryabhattai	Rhizosphere soils of peanuts, sweet potatoes, and cassava	ZnO and ZnCO3	[77]
Bacillus altitudinis, *B. subtilis*, *B. megaterium*, *B.licheniformis, Brevibacillus borstelensis* and *B. xiamenensis*	Rhizosphere of wheat grown in the eastern parts of the Indo-Gangetic Plain of India	ZnO, $Zn_3(PO_4)_2$, $ZnCO_3$	[78]
Acinetobacter pittii and *Stenotrophomonas maltophilia*	Soil and vegetation sample	$ZnSO_4$	[79]

7. ZSB WITH PLANT GROWTH PROMOTING TRAITS

It is evident that zinc solubilising bacterial inoculants can be used to increase bioavailability of native zinc for crop assimilation and therefore can help in reducing zinc deficiency in crops and human being. The effectiveness of zinc solubilising bacteria can be enhanced if they also possess plant growth promoting traits in addition to the zinc solubilisation. In order to achieve proper growth and enhanced productivity, bio augmentation of zinc solubilising microbial strains with PGP traits is imperative. It can result in enhanced growth, increase in yield and quality of crop produce due to the direct and indirect mechanisms. The direct mechanisms include nitrogen fixation, phosphate solubilisation, siderophore production, phytohormone production (IAA & ACC Deaminase) etc. The indirect mechanisms mainly comprise of the application of microorganisms as biocontrol agents, to control the plant diseases [93,94]. That includes production of HCN, Induced systemic resistance (ISR), Siderophore, antifungal activity etc. [95]. Application of Zn-solubilizing microorganisms with plant growth promoting characteristics can not only address zinc deficiencies in humans through crops, but can also be used as an alternative to chemical fertilisers and pesticides to improve crop growth and development.

Several plant growth promoting rhizobacteria have been reported earlier as they are also known to solubilise complex zinc in soil. The prime focus of agriculture has always been to improve yield through plant breeding techniques but with regards to the nutritional quality of the crops, chemical supplements or industrial fortifications have always been prioritised. Biofortification of essential micronutrients is the process to increase availability of nutrients through microbial intervention which otherwise could be achieved through agronomic practices like conventional plant breeding and biotechnology viz. genetic engineering [96,97]. Although these approaches help in enhancing the nutrients availability, nevertheless are expensive, causes environmental pollution and ethical issues [12]. Hence to overcome this issue, the application of potent PGPR agents with ability to solubilise complex nutrients can prove to be a highly effective solution. Therefore, biofortification of crops with application of PGPRs can be an efficient supplementary method to improved nutrition and yield.

8. ZINC BIOFORTIFICATION APPROACHES

The deficit of zinc in humans can only be eradicated if its concentration is enhanced in the parts of plants that are consumed on a daily basis. Hence, the popularity of biofortification of such essential micronutrients in cereal crops countries has come to existence as they are the staple food in many developing countries [13,96]. The main approaches to biofortification include plant breeding, agronomic strategies and use of biotechnology. The major intent behind biofortification is to produce varieties that have maximum uptake and accumulation of Zn in the edible portion of the crops. Agronomical strategies predominantly include zinc fertilizers which is a short term and trouble-free task. Different kinds of zinc fertilizers that are used for this process but predominantly zinc sulphate ($ZnSO_4$) is applied to increase zinc concentration in crops. Although these approaches are effective, relentless use of chemical fertilizers in agriculture leads to pollution of soil and environment. These chemicals are highly persistent and turn into complex insoluble forms in soil.

Although plant breeding strategies appears to be cost effective and sustainable, it is time consuming and complicated. Hence, there is necessity of developing a sustainable, effective and environment friendly approach to biofortification of zinc in grains. Transgenic approaches have considerable effects on biofortification process and the crop varieties with increased zinc concentration in grains [12]. The main targets for enhancing zinc concentration are the expression of ZIP family (transcription factors) and transport proteins which are responsible for zinc uptake and accumulation. However, overexpression of genes responsible for transport protein can lead to enhanced zinc uptake in the root regions [97].

9. ROLE OF ZIP FAMILY IN ZINC SOLUBILISATION

Zinc loading in grains is determined not only by the availability of zinc in the soil, but also by zinc uptake and translocation into the grains. Considering rice being the staple food, zinc fortification of rice grains could prove to be a propitious approach to diminish the zinc deficiency in humans. The expression of Zn transporting genes can be affected by ZSB inoculation in rice [10]. ZSB can regulate the uptake and translocation of zinc in plants. The zinc uptake can take place by transport mechanisms such as phytosiderophore production and ZIP family of transporters which as Zn-regulated transporters and Fe-regulated transporter like protein family [98]. The ZIP proteins are the Zn-regulated, Fe-regulated transporter like proteins that help in cellular uptake of Zn, translocation, intracellular trafficking and plant detoxification [99]. The ZIP family of transporters are responsible for the transportation of four essential micronutrients such as Zn, Fe, Cu and Mn [100,101]. ZIP family of proteins were first reported to be present in *Saccharomyces cerevisiae* and *Arabidopsis thaliana* [102,103]. However, about 15 members of ZIP protein family are found in *Arabidopsis* [101], 17 members in case of Rice (*Oryza sativa*), 12 members reported in Barley, 14 in wheat (*Triticum aestivum*) and 23 members of ZIP family reported in case of common bean [104,105]. ZIP proteins are comprised of 309 to 470 amino acids having 8 transmembrane domains. The amino and carboxyl ends of the proteins are located on the outer surface region of the plasma membrane [98].

Moreover, different plant ZIP family members have different functions when it comes to uptake and translocation. The expression of zip genes are known to vary from root to shoot to grains translocation. Particularly in Rice (*Oryza sativa*) several zip genes were reported such as: OsIRT1, OsIRT2, OsZIP1, OsZIP3, OsZIP4, OsZIP5, OsZIP6, OsZIP7 and OsZIP8 which regulate the zinc uptake from soil to root to shoot and also the storage in rice grains [106-107, 10].

These ZIP genes are also known to be induced by zinc deficiency [18,108]. The upregulation of ZIP genes are known to occur due to expression of Leu-zipper transcription factors (bZIP19 AND bZIP23) [109]. Under zinc deficit situation, expression of OsZIP1 in roots was higher as compared to shoots [110,18]. The rice plasma membrane zinc transporters mainly include OsZIP1, OsZIP3, OsZIP4, OsZIP5 and OsZIP8 which are also induced by zinc deficit conditions [111]. Furthermore, overexpression of OsZIP4 and OsZIP5 leads to increased zinc accumulation in roots but decreased accumulation in shoots [106]. From germination to grain filling, expression level of all these rice ZIP genes was differed. Even though OsZIP1 and OsZIP3 are constitutively present and expressed, the expression of OsZIP3 is generally localised in the area of nodes, therefore it is known to be responsible for translocation of zinc and its distribution to other developing tissues of the plant [112]. A recent report opined that the Zn transporter OsZIP9 is responsible for the uptake of Zn in zinc deficit and hydrophonic conditions [105].

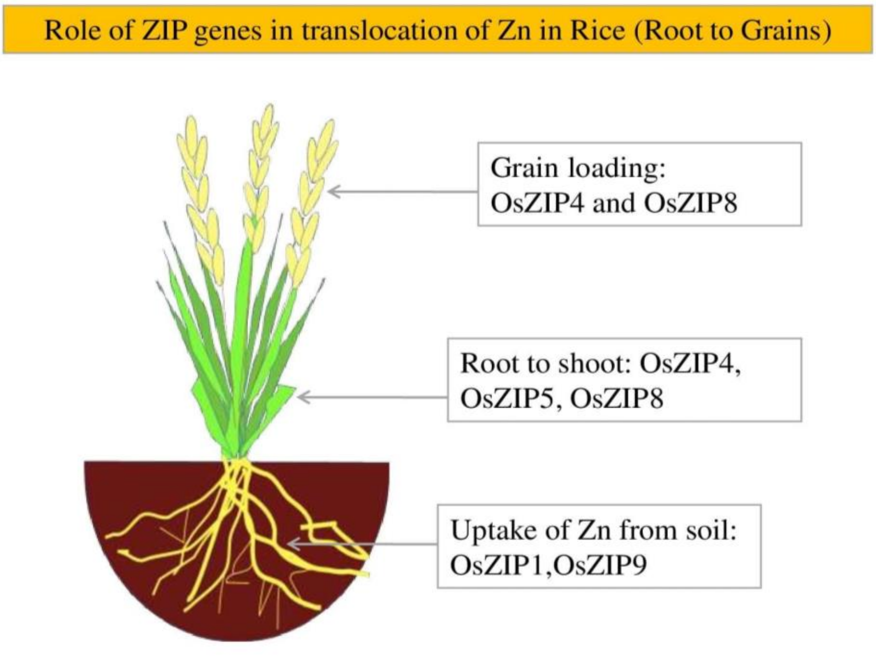

Fig. 2. Role of ZIPs in rice

Several reports suggest OsZIP1 is responsible for Zn uptake from soil [113], however the exact physiological functions of these ZIP genes and their role in Zinc uptake by plants remains poorly understood. Although the ZSBs are known to produce organic acids in their rhizospheric region to solubilise zinc and facilitate their uptake by the roots. ZSB can confer resistance on plants against specific abiotic stressors; consequently, enhancing ZSB density in the plant rhizosphere may serve as a viable substitute strategy to boost host plant growth and productivity [7]. However, to understand their role in regulation of expression of ZIP genes is still remains undefined. To elucidate the interaction between the zinc solubilizers and Zn transporters genes can help in eliminating zinc deficiency and improving zinc absorption by plants. ZSB inoculation of rice seedlings may regulate the Zn transporters protein expression through zinc assimilation. However, more research in this field is highly essential to understand the interactions and how it is helpful for zinc fortification.

10. CONCLUSION

The Zn deficiency is prominent in soil-plant system which leads to inadequate levels of zinc in humans. To improve the deficiency of zinc in soil chemical fertilizers are being supplemented, nevertheless they get converted into an insoluble complex that cannot be uptaken by the plants. In an attempt to increase the soluble or available zinc in soil, application of potent zinc solubilising bacteria can prove to be really beneficial to improve zinc nutrition in soil, plants and hence in humans. ZSBs solubilise zinc by acid production, chelation, production of amino acids, vitamins, proton extrusion etc. ZSBs are known to influence the expression of zinc transporters proteins belonging to ZIP family that help in its uptake and translocation. ZSBs possessing plant growth promoting traits such as nitrogen fixation, phosphate solubilisation etc. can potentially be an organic, environmentally friendly and cost-effective approach to Zinc fertilizers, that can not only increase the zinc availability in soil but also can improve the nutrition and help in the growth of plants.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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