Seed nutripriming with zinc is an apt tool to alleviate malnutrition

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Abstract More than 2 billion people worldwide suffer from micronutrient malnutrition, sometimes known as hidden hunger. Zn malnutrition affects around a third of the world's population. The physicochemical features of soil, which limit the availability of Zn to plants, cause Zn deficiency. The eating habits of certain populations are more depended on Zn-deficient staple foods. Due to the high expense and certain interventions such as diet diversification, zinc supplementation and food fortification cannot be achieved in disadvantaged populations. Biofortification is the most practical technique for alleviating Zn malnutrition. Seed priming with nutrients is a promising biofortification approach for edible crops. Seed nutripriming with zinc is a cost-effective and environmentally benign approach of biofortification. Seeds can be nutriprimed with Zn using a variety of methods such as Zn fertilisers, Zn chelated compounds and Zn nanoparticles. Nutripriming with nanoparticles is gaining popularity these days due to its numerous advantages and vast biofortification potential. Seeds enriched with Zn also aid plant performance in Zn-deficient soil. Zn an essential trace element can regulate physiological, biochemical and molecular processes of plant cells and thus can enhance

germination, growth, yield and bioavailable Zn in edible crops. Moreover, zinc emerges as an important element of choice for the management of COVID-19 symptoms.

Keywords Biofortification · Chelators · Fertilisers · Micronutrient · Nanoparticles · Seed germination · Photosynthesis

Introduction

Mineral nutrients are inevitable for the normal growth, development and reproduction of plants and animals including humans. At least 14 mineral elements are indispensable for plants (White & Brown, 2010) while humans require 23 mineral elements (Huang et al., 2020; White & Brown, 2010). Zinc (Zn) a chalcophile with atomic number 30 is a transition metal and ranks 23rd in abundance on earth (Broadley et al., 2007). It is an essential micronutrient required in trace and plays catalytic, structural, regulatory and signalling roles in all organisms (Gibson, 2012). It is the sole metal present in all six enzyme classes including oxidoreductases, transferases, hydrolases, lyases, isomerases and ligases (Barak & Helmke, 1993; Majumder et al., 2019). It is also present in transcription factors such as zinc finger family of transcription factors, thus having a role in gene expression (Andresen et al., 2018;

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Heidari-Beni et al., 2021). It is essential for DNA replication and transcription as RNA polymerase and DNA polymerase need Zn for their activity (Chanfreau, 2013; Wu & Wu, 1987). In physiological conditions, it is a non-redox active element due to a complete d shell of electrons (Yruela, 2013), making it suitable to perform diverse biological roles (Ishimaru et al., 2011).

Green revolution has increased the yield of staple food crops so as to feed the growing population. But the unanticipated outcome of this achievement was micronutrient malnutrition (Graham et al., 2012). Worldwide, above 2 billion people suffer from micronutrient malnutrition or hidden hunger and it has negative impact on the socioeconomic status of a country (Bailey et al., 2015). Among micronutrient malnutrition, Zn malnutrition is a major threat affecting both plants and human health. Globally, over 30% of the people is suffering from Zn deficiency, majority in developing countries due to dependence on monotonous staple food such as cereals, which are inherently low in bioavailable Zn (Impa et al., 2012; Cakmak & Kutman, 2018).

The present state of coronavirus disease 2019 (COVID-19) pandemic, an acute respiratory disease, is currently devastating the socioeconomic condition of the world. The risk factors include poor nutrition, pre-existing non-communicable diseases with a compromised immune system, which becomes prone to severe infection and eventually leads to death due to pneumonia. Zn supplements are administered along with other therapeutic agents in COVID-19 treatment (Derwanda and Scholz, 2020; Khayyat-zadeh, 2020; Muscogiuri et al., 2020; Rahman & Idid, 2020; Skalny et al., 2020) as it is effective in antiviral immunity (Read et al., 2019). To ward off the virus, Zn^{2+} ions can inhibit RNA-dependent RNA polymerase, which is needed for the replication of these viruses (de Velthuis et al., 2010) and Zn finger antiviral proteins will efficiently bind and degrade the viral RNA that invade a host cell (Luo et al., 2020; Meagher et al., 2019).

To alleviate Zn malnutrition, various approaches like diet diversification, Zn supplementation, food fortification and biofortification are implemented. However, the most feasible, sustainable and cost-effective approach is biofortification, so that it reaches to the marginalised population. Biofortification is the method of enriching edible portions of food crops with

bioavailable vitamins and micronutrients. It comprises of three strategies, agronomic biofortification, plant breeding approach and transgenic biofortification (Garg et al., 2018).

Agronomic biofortification is the application of Zn-containing compounds (as fertilisers, chelated compounds, nanoparticles) to soil, plant or seed and is a rapid and effective method of biofortification (Valença et al., 2017). In plant breeding, nutrient-rich parent lines are identified and crossed with modern high yielding but nutritionally poor varieties, to produce high yielding and nutritionally enriched varieties (Saltzman et al., 2017). Various recombinant technologies like gene silencing, overexpressing or gene insertion from another taxon can be employed to biofortify edible crops with essential nutrients (White & Broadley, 2011).

Seed priming is a practical, profitable, simple, powerful method, comprising of hydrating seeds in a controlled way to initiate many metabolic pathways, and further these hydrated seeds are dried back to their original weight before sowing (Farooq et al., 2006; Jisha et al., 2013). An agronomic approach to tackle the nutrient deficiency of plants as well as in humans is to treat the seeds with the deficient nutrient. Thus, seeds can be treated with macro- and micronutrients in order to reduce the nutrient deficiencies (Atar et al., 2020). In addition to this, seed priming with micronutrient improves the nutritional components, such as protein content (Rehman et al., 2015; Seddigh et al., 2016), and reduces antinutritional factors like Cd and phytate (Slamet-Loedin et al., 2015). The present review focuses on seed priming with Zn compounds (Zn nutrimpriming) as an effective methodology for biofortification of staple food crops.

Zinc in soil and factors affecting phytoavailability of Zn

The Zn present in the soil comes through natural and anthropogenic activities. The weathering of rock is the principal natural source, while industrial and agricultural activities such as smelters and Zn-rich fertilisers are the anthropogenic sources. The nature of parent rock, soil type, soil order, pH, climatic factors, moisture content, microbial and human activities contribute generously to zinc present in the soil (Tsonev and Lidon, 2012). In soil, Zn occurs in five

different forms, water-soluble form, exchangeable form, non-exchangeable form, adsorbed or chelated organic form, chelated to primary weathering minerals. The absorption–desorption processes between the soluble and adsorbed forms contribute to the available Zn in soil. The total Zn in regular soil is within the range of 10–300 ppm. The average amount of Zn in the soil is about 50 ppm. The total Zn present in the soil is not readily available for plants. Only a tiny proportion of the soil Zn is phytoavailable. This phytoavailable Zn can be determined by extracting Zn with DTPA (diethylenetriaminepentaacetic acid). Thus, in a given soil the DTPA-extractable Zn corresponds to phytoavailable Zn present in that soil (Sharma et al., 2013). Zn deficiency is indicated as a soil having less than 0.8 ppm DTPA-extractable Zn (Wissuwa et al., 2008).

Various factors affect the phytoavailability of Zn in soil. These factors include the pH, redox reactions, organic matter content, clay content, humus content, cation exchange capacity, microbial activity, soil structure, water content and interactions with other elements. These factors either alone or in various combinations impede the availability of Zn to the plants. The pH of the given soil contributes well to the solubility of Zn. In acidic pH below 7.7, the Zn is present in the soil as divalent cation Zn^{2+} , a readily available form for plants. In basic pH, between 7.7 and 9, Zn is seen as monovalent cation ZnOH^+ , and to some extent plants can absorb this form; above 9, it is seen as $\text{Zn}(\text{OH})_2$. In alkaline soil, the phytoavailability of Zn in soil decreases sharply; usually, the Zn present will be sorbed and may not be readily available. When CaCO_3 is present in the soil, the Zn present in the soil gets adsorbed to it in a non-exchangeable form, and the formation of insoluble calcium zincate also occurs. Moreover, the soil pH increases; thus, overall, the calcareousness decreases the availability of Zn in this soil (Prasad et al., 2014).

In a general view, the presence of organic matter in soil increases the phytoavailability of Zn. Organic matter in soil can either solubilise the Zn or fix the Zn in soil. The solubilised form of Zn is readily available to plants, while the fixed one is not available for plants (Dhaliwal et al., 2019). The principal component analysis done by Baran et al. (2018) revealed that organic carbon is an essential factor that determines the phytoavailability of Zn in soil. According to the differential solubility, organic matter in soil is divided

into fulvic acid, humic acid and humin. Usually, the Zn bound to them is in a locked form and is least available for plants. However, the Zn present in the fulvic acids is more mobile and available for plants due to its high mobility and hydrophilicity (Benedet et al., 2020). Organic matter can also influence the cation exchange capacity (CEC) of the soil. CEC is the potential of the soil to hold and exchange positively charged ions. When the CEC of soil is high, the exchangeable form of Zn present in the soil can be available for plants. Karimi et al. (2019) could increase the availability of Zn in calcareous saline soil by increasing the organic matter and cation exchange capacity of soil by the application of biochar.

The soil microorganisms such as zinc solubilising and mobilising bacteria and many arbuscular mycorrhizae can solubilise the Zn in the rhizosphere by acidifying the region by secreting phytosiderophores or by secreting phenolics. Thus, if the factors affecting their growth are suitable, they can increase the phytoavailability of Zn (Singh & Prasanna, 2020). The application of zinc solubilising *Enterobacter* sp. MN17, along with other Zn application methods, increased chickpea's yield and quality (Ullah et al., 2020). The soil structure and its water retention capacity have an essential role in maintaining phytoavailable Zn in the soil. The porous and well-aerated soil with good moisture content can make Zn available to a certain extent. The presence of clay also reduces the availability of Zn. At the same time, flooding may create an anaerobic condition in the soil and interfere with Zn's availability. Even though it increases the Zn content initially, later insoluble Zn contents are formed (Rehman et al., 2018). An analysis from 153 drylands indicated a decrease in total and soluble Zn (Moreno-Jiménez et al., 2019).

Phosphorous in the soil can interfere with the availability of Zn to the plants from the soil. In both acidic and alkaline soil, the addition of phosphorous decreased the DTPA-extractable Zn, and the root and the shoot Zn content were also decreased in the wheat plant. This decrease of Zn in tissue concentration was more in alkaline soil than the acidic soil (Chen et al., 2019). Upon application of phosphorous, the concentration of Zn in various staple crops such as wheat and maize decreased to the extent of 16.6% and 20.2%, respectively. This reduction in Zn content is corroborated with the reduction in arbuscular mycorrhizal

colonisation of roots (Zhang et al., 2021). Nitrogen positively influences the soil Zn availability as well as the grain Zn content. A field study conducted by Jaksomak et al. (2017) in 5 rice varieties indicated an increase in grain Zn and yield in low-grain/high-yield varieties while increased the yield and decreased the Zn in high Zn/low yield varieties.

Zinc from soil to plants

The mobility of Zn from the rhizosphere to the root system of a plant is determined by the plant type, root characteristics, physicochemical properties of soil and various plant–microbe interactions. The roots absorb Zn as a divalent Zn ion form. Like all the nutrients, the need for Zn by plants during various phases of the life cycle is different. Thus, according to the genetic makeup and physiological need for Zn, plants can increase the solubility and absorption of Zn from the soil by acidifying the rhizosphere. In plants, the root can exudate proton, organic acids like citric acid, malic acid and oxalic acid. Plants can actively absorb the Zn by hyperpolarising the root cell plasma membrane with the aid of ATPase. In cereal crops, there is an additional mechanism and it is by releasing phytosiderophores into the soil, which forms complexes with Zn, aiding in the absorption of Zn (Gupta et al., 2016). Arbuscular mycorrhizae (AM) can alter the physicochemical properties of soil, and through phosphatase, dehydrogenase activities and releasing glomalin glycoprotein, they facilitate the uptake of Zn from the soil. A field study in maize for increasing grain Zn content by the activity of zinc solubilising bacteria and AM mycorrhizae has found promising results (Suganya et al., 2020).

Within the plant, transporter proteins are necessary for translocation and storage of Zn in edible portions. These proteins play an essential role in the translocation of metal ions into and out of the cell, microcompartments, and sequestering these ions in vacuoles to act as a reservoir or reduce toxicity. Mainly three transporter systems are elucidated for Zn transport. They are the ZIP (zinc–iron permease or ZRT, IRT-like proteins) family of transporters seen on the plasma membrane. The CDFs (cation diffusion facilitator) like MTPs (metal tolerance protein), seen on tonoplasts and HMAs (Heavy Metal ATPase) a P-type ATPase, localised on the plasma membrane, tonoplast

and endomembrane system (Caroli et al., 2020). Usually, Zn is transported within the plant as Zn^{2+} or complexed with protein, amino acids and organic acids. In the xylem, translocation of Zn occurs mainly as Zn^{2+} or complexed with histidine or nicotianamine (NA) while in the phloem, Zn is mostly as complexed with small proteins and NA. Zn can reach the storage tissues via xylem or phloem (White & Broadley, 2009).

Plants require optimum concentration of Zn for the growth and functioning of specific metabolic processes. The concentration of Zn in many plants ranges between 30 and 100 mg Zn/Kg dry weight and above this is toxic, even though some hyperaccumulators possess above this range (Noulas et al., 2018). The concentration of Zn below 15–20 µg per gram dried leaves shows Zn deficiency (Heidari-Beni et al., 2015; Mitra, 2015). It is important in chlorophyll biosynthesis, IAA metabolism, pollen formation, maintenance of membrane integrity, protection against photooxidative damage (Noulas et al., 2018) and takes part in the repair of PSII, by replenishing the photodamaged D1 protein (Li et al., 2020; Woodson, 2019).

Zinc deficiency in plants occurs due to the lack of phytoavailable Zn in the soil. The phytoavailability of Zn in the soil decreases with high pH, calcareousness, very high and low organic content, clay, high phosphorous content (Alloway, 2009; Hafeez et al., 2013; Pourmirzaiee et al., 2018). Growing crop plants in such soils decrease its growth, yield and quality. The deficiency of Zn in plants causes stunted growth, chlorosis, smaller leaves, sterile spikelets (Das et al., 2018), decrease in fruit size, inhibition in shoot elongation, reduced Cu/Zn superoxide dismutase (SOD) activity, enhanced photooxidation, oxidative damage of membranes, proteins, phospholipids, chlorophyll molecules, nucleic acids, SH group containing enzymes, IAA inhibition (Zaman et al., 2018), synthesis of impaired protein, increase in ROS, decrease in detoxification mechanism (Cakmak, 2000). A decrease in chlorophyll content, lower chl *a*: *b* ratio, reduction in PS II per leaf area, impaired quantum efficiency of PS II, in effect a decline in photosynthetic performance occurs in Zn-deficient plants (Chen et al., 2007).

Zn in edible portions of crops

The plants growing in similar conditions differ significantly in absorption, translocation, accumulation and storage of Zn. The rich sources of Zn within the plants include leafy vegetables, and the least available source includes cereals. It may be due to the immobile nature of Zn within the plant tissue, primarily through the phloem. Usually, the seeds, fruits, tubers are phloem fed tissues; thus, the amount of Zn in these edible portions will be low. When compared to the cereals, the legumes contain more Zn. Amaranthaceae, Brassicaceae and Salicaceae accumulate more Zn content, whereas the Poaceae, Solanaceae and Linaceae acquire least Zn content (Akhtar et al., 2019; Gregory et al., 2017). Even though fruits are poor sources of Zn, pomegranate is rich in Zn. It contains Zn to the level of 9.97–17.29 mg kg⁻¹ fresh weight (Tozzi et al., 2020). A study conducted in 8 citrus fruit cultivars found that the Zn concentration within them is in the range of 0.10–0.24 mg/100 g fresh weight (Czech et al., 2020). The Zn in edible portions of plants is dependent on the genetic makeup and environment of the plant.

Zinc in human

The recommended daily intake of Zn, depending on age, gender, diet is between 3 and 16 mg Zn per day. No long-term storage system is present for Zn in humans, so daily dietary intake is necessary to maintain Zn in acceptable range (Hotz & Brown, 2004). Zn is obtained by humans via a wide range of foods. Animal-based foods are more nutritious and bioavailable than plant-based foods. Zn is found in abundance in oysters. Beef, hog, lamb, chicken and their products are high in Zn content than other meats. Milk and milk products can also provide Zn to humans. Zn is also found in leafy vegetables, beans, tubers and cereals. Plant products, on the other hand, are less bioavailable due to the presence of antinutrients such as phytate (McClung, 2019; Chasapis et al., 2020). The physiological requirement of Zn is high during pregnancy, infancy, lactation and adolescence. Zn plays important role in immune system, sensory system, reproduction, oxidative stress, apoptosis, neurobehavioural development and also acts as a

neurotransmitter (Gammoh & Rink, 2019; Prasad, 2008; Wani et al., 2017).

In infants and children, Zn deficiency results in compromised neuro-behavioural function. Acrodermatitis enteropathica is a genetic disorder that is contributed by poor Zn absorption in humans (Ogawa et al., 2018). In humans, Zn deficiency leads to learning disability, decrease in physical growth, delay in sexual maturity, vulnerability to diarrhoea and pneumonia, malfunctioned immune system and increase in infections and mortality. Among elderly, Zn deficiency results in chronic non-healing ulcers, impaired taste sensitivity and compromised immune system (Chasapis et al., 2020).

Causes of Zn malnutrition

Zinc deficiency ranks fifth in developing countries and eleventh in world as risk factor responsible for morbidity and mortality in humans (WHO, 2002). The most important reason behind Zn deficiency is intake of Zn-deficient diet or consumption of food with low bioavailable Zn, such as food with high phytate content (Clemens, 2014). Zn deficiency is also caused by increased demands, malabsorption, impaired usage and increased losses. Malnutrition could be caused by any of these conditions, alone or in combination. These issues might also occur as a result of physiological or pathological situations that necessitate higher Zn levels. The bioavailability of Zn might potentially be hampered by the use of certain medications (Hotz & Brown, 2004).

Some people are hesitant to ingest animal-based foods because of religious beliefs. Vegans and vegetarians face the same difficulties. Zn availability in a plant-based diet is influenced by soil Zn levels as well as antinutrients such as phytate, calcium and polyphenols (Gupta et al., 2020). The majority of people in developing and impoverished nations rely on one or more cereal crops as a main meal. The majority of people in these countries rely on their agricultural fields for food and survival. Their dietary variety is relatively limited. They are not able to afford the variety of food items such as animal-based food which are rich in Zn. Moreover, the Zn condition of the soil plays a critical role in Zn deficiency. Typically, soil Zn deficiency corresponds to Zn malnutrition in certain parts of the world. Zn deficiency affects almost half of all cereal cultivation regions, and growing these cereal

varieties in Zn-poor soil reduces the amount of bioavailable Zn in these genetically deficient Zn crops. After milling and polishing, cereal grains such as rice and wheat are commonly consumed. As Zn concentration is higher in the hull, bran and embryo of grains than in the endosperm, the bioavailability of Zn from such crops is reduced further (Cakmak & Kutman, 2018).

Rice–wheat cropping is one of the most important agricultural systems in South Asia. Some of the causes behind Zn deficiency in these regions include extensive cropping, injudicious use of fertilisers such as N, P and K, and poor management of on-farm residue because these cropping systems are typically inundated for the majority of the growing season. Zn insufficiency worsens due to physicochemical parameters of soil, such as soil pH and Zn solubility (Nadeem & Farooq, 2019). Humus in the soil binds Zn to its particles. Compost and charcoal use in agricultural soil can raise humic and fulvic acid levels, lowering bioavailable Zinc (Li et al., 2019). Organic manure applied in an indiscriminate manner can reduce Zn bioavailability by forming insoluble compounds with Zn and altering soil pH. Substantial use of pig dung reduced the Zn concentration of Brazilian soil (Benedet et al., 2020).

Seed priming

The embryo enclosed within a seed is a future plant. The resources given to a seed can increase the ability of the plant to become successful in its realised niche. Seed priming is a promising technology, to improve the performance in field and nutritional status of crops. In nutripriming, seeds are soaked in a solution containing nutrients to start pregerminative metabolic events without radical protrusion, after which seeds are dried closer to their original weight (Farooq et al., 2019).

Seed treatment or seed invigoration can be achieved by two methods: seed coating and seed priming or nutripriming. In seed coating, a more or less continuous layer of finely ground solids or liquids containing dissolved or suspended solids is covered all over the seed. In nutripriming, seeds are primed with nutrients by soaking in an appropriate nutrient solution for a specific duration of time (Farooq et al., 2019). By the technique of nutripriming, along with the nutritional

advantages, biochemical achievements of priming can also be realised (Lutts et al., 2016). It helps the crop to meet its micronutrient requirements and improves germination, seedling emergence, stand establishment, yield, grain micronutrient quantity (Haider et al., 2020; Imran et al., 2015), resistance to abiotic and biotic stresses (Cabot et al., 2019; Rehman et al., 2012).

When compared to foliar spray and soil application, the benefits of nutripriming are numerous. The majority of fertilisers are mined, and these sources are limited. There is also environmental concern, as mining pollutes the environment (da Cruz et al., 2019). When nutrients are added to soil, they must pass through multiple huddles created by the soil's physicochemical qualities in order to reach the plant. Foliar spray can be used to get rid of the huddles that soil creates. However, the quantity required is large, and it must be sprayed at regular intervals of growth phases, and phytotoxicity is a serious worry. However, neither of these strategies can overcome the non-synchronised emergence of seeds, which is a key obstacle faced by changing environment and nutrient deficiency in seeds. Nutripriming can help to overcome all of these issues.

Nutripriming is less expensive and uses less nutrients, making it both cost-effective and environmentally beneficial. It can also aid in the uniform emergence and stand establishment of seedlings, stress tolerance as well as improve quality and quantity of yields (Majda et al., 2019). The concentration and duration of nutripriming are two essential characteristics that influence it and it varies from crop to crop, depending on its genetic makeup. Priming in larger concentrations for longer periods of time resulted in a decrease in growth metrics in most crops, possibly due to phytotoxic effects (Nciizah et al., 2020). As a result, preliminary research must be conducted to determine the optimal nutrient content and duration for improving crop growth, production and quality.

Various sources of Zn for nutripriming

The various Zn sources used in seed priming include inorganic Zn sources, organic Zn sources, chelated Zn sources and Zn nanoparticles (Zn-NP). The inorganic source includes zinc sulphate (ZnSO_4), zinc sulphate heptahydrate ($\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$), zinc chloride (ZnCl_2),

zinc nitrate (ZnNO_3), zinc carbonate (ZnCO_3) and zinc oxide (ZnO). ZnSO_4 and $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ is the most commonly used priming agents due to its solubility, less reactivity soil components and cheaper rate. The most common synthetic chelated form of Zn is Zn-EDTA, wherein the metal ion is coordinated with the chelating agent (Fig. 1). The quantity of soluble part of Zn present in all the above compounds varies (Naik & Das, 2007; Ostad-Ali-Askari et al., 2017). The synthetic Zn chelators have many ill effects like low biodegradability, quick photodegradability and release of toxic agents on application in high amounts. It is also costly. So organic Zn chelators like Zn amino acids are also acquiring prominence as a priming agent. Zn amino acid complexes such as $\text{Zn}(\text{His})_2$, $\text{Zn}(\text{Met})_2$, $\text{Zn}(\text{Gln})_2$, $\text{Zn}(\text{Gly})_2$, $\text{Zn}(\text{Arg})_2$ are commonly used for priming (Mirbolook et al., 2020).

Nanoparticles are attaining attraction nowadays as they have many superior characteristics when compared to the traditional sources of nutrients. Some of such traits are their high surface area-to-volume ratio, high stability, high adsorption, increased surface reactivity, etc. Thus, a low dosage of application can have a visual impact on increased growth, yield and biofortification of crops (Mittal et al., 2020; Rastogi et al., 2017). The zinc nanoparticle (Zn NP) is one of the widely used NP in agricultural sector. It can be synthesised chemically by using chemical reagents (Neto et al., 2020) or biologically with the aid of microorganisms (Sabir et al., 2020) or plant extracts (Sabir et al., 2014). When used for priming and biofortification, the cost-effectiveness as well as the overall activity and effectiveness are usually considered before selecting a Zn source as a good priming agent.

Effect of Zn enrichment in plants

Seed priming influences plants positively and helps the plant to tide over the hazards and difficulties that it encounters during its life cycle. At every stage of the life cycle, priming has significant influence and it helps the plant to attain its biotic potential. Zn nutrimpriming has beneficial impact on germination parameters, seedling establishment, various yield attributes and Zn content in edible tissues (Farooq et al., 2012), and also many metabolic processes get stimulated (Gupta et al., 2016). The use of nutrimprimed

seeds in Zn-deficient soils are more efficient, as seeds with high Zn content perform better in Zn-deficient soil than seeds with a smaller Zn content (Cakmak & Kutman, 2018). There is a trend of increase in Zn content in edible portions on increasing the seed treatment concentrations of Zn. But at higher concentrations, germination and growth are inhibited due to phytotoxicity. Thus, before considering a priming concentration genotoxic studies must be done. One such approach is to study the genotoxicity, by analysing the mitotic index and nucleolar activity of root tips (Carvalho et al., 2019; Reis et al., 2018).

Zinc in germination and seedling establishment

Seed priming increased the germination rate, reduced mean germination time and provided synchronised germination and early establishment of seedlings in crop plants. When mungbean seeds were nutrimprimed for 6 h in 0.1 M ZnSO_4 solution, germination increased by 53% when sown in a sandy loam soil with an alkaline pH of 8 (Haider et al., 2020). This may be due to the involvement of Zn in activating many enzymes needed for key metabolism like those involved in anaerobic respiration like alcohol dehydrogenase and is also crucial for the production of proteins (Cakmak & Kutman, 2018). During seed priming, the supplied Zn is efficiently transported to the inner regions of the seed from the husk, increasing its availability to the region where it is required the most. This can be visualised by dithizone (DTZ) staining of seeds. When rice grains were treated with this stain, regions with Zn showed red colour and the intensity increased proportionally with the increase in Zn concentration (Prom-u-thai et al., 2012). This is because DTZ, a Zn chelating agent on reacting with Zn forms Zn-dithizone complex which is red in colour (Durate et al., 2016).

Zn-induced auxin production may be the reason for cell elongation and cell division, thus helping in root and shoot elongation. The distribution of Zn in coleoptile and radicle gives further proof for this. On germination, Zn present in the seeds is mobilised to growing regions of coleoptile and radicle and gets concentrated more at the tips. This feature shows the requirement of Zn in enzymes, carbohydrate metabolism as well as in transcription and translation, thus aiding in the increase in various growth parameters (Broadley et al., 2011; Ozturk et al., 2006). During

Fig. 1 Effect of Zn nutripriming in plants

DNA replication for the formation of initiation complex and replication fork, MINICHROMOSOME MAINTENANCE (MCM) proteins are needed. They possess various domains including a zinc finger domain for their activity. Along with this protein, several other proteins with Zn finger domain are also necessary for replication (Shultz et al., 2007). Also during cell division Zn is necessary for the polymerisation and stability of microtubules (Domart et al., 2020).

Transcription factors regulate gene expression and thus have role in development, signal transduction and metabolism. GATA Zn transcription factors are DNA binding proteins which regulate various developmental processes in plants including flower development (Zhu et al., 2020). The role of GATA Zn finger transcription factor, BLUE MICROPYLAR END 3 (BME3) in breaking seed dormancy, is well documented in *Arabidopsis* plant. It positively influences the transition from dormancy to germination, by enabling the radicle to come out by resisting the

various mechanical constraints that block germination. This can be correlated with the observation that seeds with malfunctioned BME3 showing deeper dormancy when compared with the normal populations (Liu et al., 2005). On priming the seeds with Zn, this metal may possibly influence this transcription factor and thereby enhance the germination parameters.

During germination ROS are produced continuously as a result of the metabolic activities occurring in mitochondria, peroxisomes, glyoxysomes and chloroplast. Although ROS accumulation can be harmful, low levels of the same can provide disease resistance, apoptosis of aleurone layer, deterioration of endosperm, cell signalling and maintenance of redox potential. The level of ROS should be maintained between a threshold level called “oxidative window” for breaking the seed dormancy. Below it, the seed will remain in dormant stage, and above this level, it results in production of anomalous seedlings. Thus, in order to break dormancy and increasing the seed vigor, the cell’s antioxidant machineries should perform perfectly and flawlessly. Hence, Zn-containing SOD and catalase enzymes appear to help the seed to increase its vigor by controlling the ROS levels (Ma et al., 2017). The possible role of Zn in germination is illustrated in Fig. 2.

Zinc in yield, yield-related traits and Zn accumulation in edible parts

The efficacy of Zn in promoting the grain yield and yield components can be inferred by analysing the productive panicle number, grains per panicle and grain weight. Through seed treatments with Zn, all these attributes can be increased (Farooq et al., 2018). In Zn-deficient soil, nutripriming of maize plants in the optimum concentration and time with ZnSO₄ solution enhanced the yield by 27% (Harris et al., 2007). In a field research done in Faisalabad and Sialkot, ZnSO₄ primed seeds enhanced the yield by 31% and 40%, respectively (Farooq et al., 2018). The use of ZnSO₄ solution to prime the rice seeds enhanced the output by 23%. (Zulfiqar et al., 2020). In the case of chickpea, priming with ZnSO₄ solution improved the yield by 24% and 15% in the desi and kabuli varieties, respectively (Ullah et al., 2020). Zn seed priming was the most efficient strategy for increasing wheat grain production in rice–wheat cropping systems, increasing output by 56 per cent

in conventional tillage and 60 per cent in conservation tillage (Nadeem et al., 2020). The reason behind this can be deduced by the fact that Zn is necessary for the pollen tube growth and fertilisation by facilitating pollen–stigma interaction (Pandey et al., 2006). For effective fertilisation and seed setting, the pollen from the androecium has to reach the female gametophyte present in the gynoecium, and for this the pollen tube grows and moves through the transmission tract of the style. The extracellular space needed for the pollen tube growth is produced by programmed cell death (PCD), the *NO TRANSMITTING TRACT* gene encoding a C2H₂/C2HC zinc finger transcription factor facilitates this (Cascallares et al., 2020). In addition to this, the movement is also facilitated by the expression of *CENTRAL CELL GUIDANCE (CCG)* gene encoding a transcription factor with a conserved N terminal zinc β-ribbon domain in the central cell of the mature female gametophyte (Chen et al., 2007; Li & Yang, 2020; Wang et al., 2010). Thus, Zn has a prominent role in effecting the fertilisation and seed set.

The greater growth attributes reflected in plants as a result of Zn are due to the involvement of Zn in photosynthesis. Carbonic anhydrase, a Zn metalloenzyme, shows pivotal role in photosynthetic organisms as it is crucial for the activity of the enzyme Rubisco. Carbonic anhydrase catalyses the reversible conversion of bicarbonate to CO₂, the substrate needed for Rubisco (Dimario et al., 2017; Qiao et al., 2014). Thus, the role of Zn in the activity of carbonic anhydrase and the indirect influence in the rate of photosynthesis is evident by the decrease in carbonic acid concentration, carbonic anhydrase mRNA as well as photosynthetic rate during Zn-deficient condition (Sasaki et al., 1998; Polishchuk et al., 2021). The aspects discussed above are illustrated in the fig. 2.

Aldolase, a Zn-dependent enzyme, is vital for growth and development of all organisms including plants. It plays an essential role in carbohydrate metabolisms by catalysing key reactions in reductive pentose phosphate cycle, metabolic processes such as Embden–Meyerhof–Parnas (EMP) pathway and gluconeogenesis (Lv et al., 2017). Hence, it can be inferred that this enzyme assists in enhancing photosynthetic capacity, growth rate and thus biomass increase by hastening the regeneration of RuBP. The most important part of the seed is embryo, and it is equipped with all the factors needed for germination and survival. As a result, this propagule is a store

Fig. 2 Possible role of Zn in nutriprimed plants. The possible role of Zn in pollen tube growth, in increasing bioavailability of Zn, increasing growth of the plant by influencing photosynthesis and increasing seed germination. Abbreviations: Zn-zinc,

HMA's-heavy metal ATPase, IRT-iron-regulated transporter, MCM-MINICROMOSOME MAINTAINANCE protein, CAT-catalase, SOD-superoxide dismutase, ROS-reactive oxygen species, T.F-transcription factor

house of essential minerals like Zn needed for the activation of enzymes, light harvesting and turgor maintenance needed during germination (Lu et al., 2013).

Possible roles of priming in influencing the increase in Zn level in plants

To fulfill any biofortification approach, a thorough knowledge of the transporter system is very essential. Transporter proteins are necessary for the

translocation of metal ions into and out of the cell, microcompartments and for sequestering these ions in vacuoles to act as a reservoir or to reduce toxicity. Mainly three transporter systems are elucidated for Zn transport. They are the ZIP (zinc–iron permease or ZRT, IRT-like proteins) family of transporters seen on plasma membrane. The CDFs (cation diffusion facilitator) like MTPs (metal tolerance protein), seen on tonoplasts and HMAs (heavy metal ATPase) a P-type ATPase, localised on plasma membrane, tonoplast and endomembrane system (Caroli et al., 2020).

On seed invigoration (seed priming or seed coating) with Zn, an increase in yield factors was noticed, which may be due to increased expression of Zn transporters like HMAs. There is evidence for the expression of HMAs (HMA9) transporter proteins in anther of rice and *Arabidopsis* on application of Zn. The increased Zn in anther has many positive aspects such as increased pollen fertilisation and seed set as discussed earlier. Thus, it could be concluded that these transporters translocate Zn into androecium to bring about increase in yield parameters (Lee et al., 2007). This can be confirmed by the male sterility of *nas4x-2* mutant line of *Arabidopsis* during Zn deficiency. In these mutants, the nicotinamine (NA) was completely absent, affecting NA-mediated transportation of Zn to anthers via the transporters (Schuler et al., 2012).

BRUTUS (BTS) a Zn-containing protein is able to regulate the expression of genes needed for Zn translocation and accumulation. BTS is an E3 ubiquitin ligase characterised by having a Zn finger protein domain. This ubiquitin ligase can add ubiquitin and regulate FER-LIKE DEFICIENCY-INDUCED TRANSCRIPTION FACTOR (FIT) transcription factor which aids in the expression of genes needed for Fe uptake and the genes for the transporters like IRT. Along with Fe, non-specific uptake of Zn also takes place through this transporter (Long et al., 2010). FIT can also regulate the expression of *NICOTINAMINE SYNTHASE (NAS)* genes (Rodríguez-Celma et al., 2019). The *NAS* synthesises low molecular weight chelators like nicotinamine (NA) and deoxymugeieic acid (DMA) which can chelate Zn. The Zn-NA complex thus formed aid in long distance transport of Zn via xylem and phloem into the seed (Clemens et al., 2013; Lee et al., 2011). The plant cadmium resistance 1 (PCR1) is a transmembrane protein aiding the translocation of Zn. In rice, it is present in roots at

seedling stage, on reproductive stage seen on I and II internodes and on spikelet. Hence it can be proposed that this transporter may also have role in Zn accumulation in grains (Song et al., 2015). Therefore, during seed priming this metal can certainly regulate the key genes discussed above reflecting in biofortification. The possible role of Zn nutrimpriming in increasing the Zn in edible tissues is discussed in Fig. 2.

Achievements of Zn biofortification through nutrimpriming

Seed priming with ZnSO_4 solution increased the yield and yield-related traits and grain Zn content in barley and wheat. However, an increase in concentration and time of application has negative effect on the growth and yield. This may be due to the cytotoxic effect of high concentration of Zn. Seed priming as well as seed coating of two varieties of wheat with $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ increased the stand establishment, emergence, yield and yield-related traits, and also grain Zn content in continuous two seasons of experiments (Hassan et al., 2019). In three wheat varieties, different types of Zn amino acid chelate were used to study the effect on growth, yield and biofortification efficiency. The biofortification efficiency of each varied with the source of Zn and genetic makeup of the wheat variety. The different Zn amino acid chelates used were Zn-histidine [$\text{Zn}(\text{His})_2$], Zn-glutamine [$\text{Zn}(\text{Gln})_2$], Zn-arginine [$\text{Zn}(\text{Arg})_2$] and Zn-glycine [$\text{Zn}(\text{Gly})_2$]. When compared to other priming agents, and soil application of Zn fertilisers, Zn-histidine and Zn-arginine increased grain Zn content (Seddigh et al., 2016). Seed priming with ZnSO_4 and ZnCl_2 in sugar beet increased the Zn concentration, making it a potential biofortification candidate. From this study, the Zn level increase achieved through Zn seed priming could be correlated with the increase in photosynthetic rate, transpiration and stomatal conductance of the plant (Carmona et al., 2020). Seed invigoration by priming and coating of chickpea with ZnSO_4 increased the bioavailable grain Zn content along with the yield and yield-related traits (Ullah et al., 2020).

Farooq and co-workers (2018) studied the yield and grain Zn content of aromatic rice grain based on various Zn application methods including seed

priming and seed coating in direct seeded and transplanted rice production systems. Even though there were no marked differences in yield among the treatments, there were considerable differences in grain Zn content. When compared to seed coating, seed priming was more effective in increasing the grain Zn content (Farooq et al., 2018). On calcareous soils, seed priming of rice with 0.5% ZnSO₄ solution could increase grain Zn content, when compared to control plants without any Zn treatment (Imran et al., 2015).

Seed priming with Zn is a good option to increase growth, yield parameters and grain Zn content of mungbean (*Vigna radiata* (L.) Wilczek) (Haider et al., 2020). Field trails of wheat and chickpea, using ZnSO₄ as a priming agent, increased the grain Zn content (Harris et al., 2007). A comparative study of different modes of Zn treatments in maize was done to identify the potential of each method for biofortification. The results showed that seed coating method was more effective in increasing the grain Zn content (Ladumor et al., 2019). Seeds of two cultivars of common bean “Sadri” and “Talash” were considered to analyse the influence of Zn amino acid synthetic chelators like Zn-methionine [Zn(Met)₂] and Zn-histidine [Zn(His)₂] over soil applied Zn fertilisers. The analysis revealed that Zn(Met)₂ was more efficient in increasing the seed Zn content in “Sadri” cultivar while the Zn(His)₂ was more efficient in “Talash” cultivar. Seed priming using [Zn(His)₂] and [Zn(Met)₂] increased the grain Zn concentration by 8.5–33.8 per cent and 16.5–34.3 per cent, respectively, as compared to the priming with ZnSO₄ (Tabesh et al., 2020). And it was clearly evident that Zn amino acid synthetic chelators gave better results than Zn fertilisers.

When compared to priming using ZnSO₄ as an application, ZnO-NP increased the germination, yield and biofortification of ragi (Rameshraddy et al., 2017). The combined action of ZnO-NP and FeO-NP increased nutritional factors and Zn in ragi (Mahmoud et al., 2019). This shows that Zn-based nanoparticles can bring about more positive effect of Zn biofortification. Seed priming with Zn-NP can increase the concentration of various amino acids such as glutamate and glycine, which helps in metabolism and chlorophyll synthesis and thus can improve the growth aspects as well as the nutritional status of the plants (Salama et al., 2019). In general, there are very less literature available on the usage of NP for the

nutripriming of seeds. In future, the technology of NP may play a significant role in achieving the biofortification of important crops. Zn nutripriming with Zn-NP requires only less quantity of NPs for application, and at the same time, it can show all the potential superior qualities, and hence, it will be more cost-effective and a clean technology when compared to other methods. Biofortification approaches for Zn through seed invigoration (seed priming and coating) techniques in various crops are enlisted in Table 1.

Conclusion

Micronutrient malnutrition is now recognised as a serious health and economic issue in the world, as it negatively affects the socioeconomic status of the country. Thus, it is high time to shift our agricultural practices to ensure nutrient enrichment in food grains. Zinc malnutrition is common in developing countries, due to dependence on a monotonous diet based on Zn-deficient staple food crops. The alternative approaches to meet the dietary requirement of Zn, like food fortification, diet diversification, Zn supplementation cannot be realised in these impoverished communities. The foremost method to alleviate Zn malnutrition in these regions is to biofortify the major food staple crops. Various methods of biofortification are agro-nomic approach, breeding and transgenic approaches. Seed invigoration including seed priming and seed coating is cost-effective, eco-friendly methods of biofortification. Because each plant reacts differently to each priming agent, the correct priming agent and application dosage must be standardised first. The priming agent may be hazardous to plants at high concentrations; hence, the optimal concentration has to be experimented to determine the priming agent's genotoxic dosage. No single intervention can alleviate all of the issues associated with micronutrient malnutrition; all interventions, in conjunction with state policy, should work together to address the effects of hidden hunger and bring about a viable solution.

Future prospects

Biofortification of crops with Zn needs a deeper knowledge of physiological, biochemical and molecular mechanisms of Zn transportation and activity of

Table 1 Different methods of Zn nutripriming and its effect on yield and grain Zn content

Priming agent	Plant	Soil characteristics	Application dosage	Yield (%) increase over control	Grain Zn content (%) increase over control	References
ZnSO ₄	<i>Zea mays</i> L.	Silty clay loam deficient in N, P and available Zn	1%, 16 h	27	7	Harris et al. (2007)
ZnSO ₄	<i>Zea mays</i> L.	Clay loam with pH 7.8, DTPA-extractable Zn 0.64 ppm	1%, 2 h	11	20	Ladumor et al. (2019)
ZnSO ₄	<i>Zea mays</i> L.	Clay loam with pH 7.8, DTPA-extractable Zn 0.64 ppm	2%, 2 h	16	42	Ladumor et al. (2019)
ZnSO ₄	<i>Zea mays</i> L.	Clay loam with pH 7.8, DTPA-extractable Zn 0.64 ppm	3%, 2 h	12	46	Ladumor et al. (2019)
ZnSO ₄	<i>Triticum aestivum</i> L.	Silty clay loams with pH 8.1–8.3, DTPA-extractable Zn 0.68 ppm	0.3%, 10 h	12	14	Harris et al. (2007)
ZnSO ₄ 7H ₂ O	<i>Triticum aestivum</i> L.	–	0.01 M, 12 h	34	48	Hassan et al. (2019)
ZnSO ₄ 7H ₂ O	<i>Triticum aestivum</i> L.	–	0.1 M, 12 h	20	14	Hassan et al. (2019)
ZnSO ₄	<i>Triticum aestivum</i> L.	Silt loam with pH 8.3, DTPA-extractable Zn 0.70 ppm. (Traditional tillage)	0.025 M, 16 h	56	22	Nadeem et al. (2020)
ZnSO ₄	<i>Triticum aestivum</i> L.	Silt loam with pH 8.3, DTPA-extractable Zn 0.70 ppm. (Conservational tillage)	0.025 M, 16 h	60	31	Nadeem et al. (2020)
ZnSO ₄ 7H ₂ O	<i>Oryza sativa</i> L.	Site 1- sandy loam with pH 7.6 DTPA-extractable Zn 0.63 ppm	0.5 M, 24 h	31	28	Farooq et al. (2018)
ZnSO ₄ 7H ₂ O	<i>Oryza sativa</i> L.	Site 2—silt loam with pH 7.5, DTPA-extractable Zn 0.67 ppm	0.5 M, 24 h	40	46	Farooq et al. (2018)
ZnSO ₄ 7H ₂ O	<i>Oryza sativa</i> L.	Sandy clay loam with pH 7.2, DTPA-extractable Zn 0.61 ppm	0.25 M, 16 h	23	73	Zulfiqar et al. (2020)
ZnSO ₄ 7H ₂ O	<i>Vigna radiata</i> (L.) Wileczek	Sandy loam soil with pH 8.0,	0.01 M, 6 h	35	60	Haider et al. (2020)
ZnSO ₄	<i>Cicer arietinum</i> L.	silty clay loams with pH 8.1–8.3, DTPA-extractable Zn 0.68 ppm	0.05%, 6 h	19	29	Harris et al. (2007)
ZnSO ₄	<i>Cicer arietinum</i> L.	Sandy loam with pH 8.0–8.1, DTPA-extractable Zn 0.61–0.63 ppm	0.001 M, 8 h	34	11	Ullah et al. (2020)

Zn in cells. Research has to be focused to identify all the Zn transporters and to carry out their molecular and physiological characterisation. The regulation of proteins involved in Zn accumulation should be studied at transcriptional and post translational level. Cadmium, a toxic analogue, may accumulate, as many of the Zn transporters can transport Cd in lieu of Zn. Research should be directed towards the possibility of Zn accumulation in preference to Cd. There are many Zn compounds used for priming, each crop responds differently to each source, so research must be done to find the appropriate priming agent and dosage for each crop. Zn-NP is a potential agent for biofortification, and research must be also done to find a clean and green nanoparticle which is highly efficient. Epigenetic analysis also has to be done to study the retention of priming memory and the genetic changes in continuous generations, that is, imparted by nutrimpriming with Zn compounds.

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Declarations

Conflict of interest The authors declare that they have no conflict interest.

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