https://doi.org/ 10.48047/AFJBS.6.7.2024.1858-1883

AFJBS

African Journal of Biological Sciences

Journal homepage: http://www.afjbs.com

Research Paper Open Access

Micronutrients biofortification of millets: A sustainable approach

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Volume 6,Issue 7, 2024

Received: 29 Mar 2024

Accepted : 22 May 2024

doi: 10.48047/AF5BS.6.7. 2024.

1858-1883

Abstract

Genetically differing, conventional, naturally growing, traditional, or primordial food crops were nutritionally rich especially in micronutrients. These days, micronutrients quantity from the food crops has been dropped and even a few have been missing from the edible crops since the farmers prefer to have more crop production and to make more returns. Further, the farmers are paying more attention to the application of macro elements in the soil, ignoring the importance of microelements. Lessened quantity of micronutrients in soils results in food crops deficient in micronutrients, which ultimately results in 'hidden hunger' in humans. To overcome these problems, microbial-facilitated building up of micronutrients is a novel and assuring approach for higher accessibility of nutrients to crop plants and this approach is known as biofortification. Microbial approach is receiving more consideration to upsurge phyto-obtainability of micronutrients, specifically iron and, zinc in the millet crops. Exploitation of distinct types of potential microbes (bacteria and fungi) that encourage plant growth and development is befitting as an efficient and effective tactic to replace manmade fertilizers, supplements, and pesticides. Beneficial microbes use various mechanisms to mobilize the micronutrients from soil to plants such as organic acids production, acidification, metal chelation, and exchange reactions. This review focuses on millets importance and managing the uptake and mobilization of micronutrients (iron/zinc) using microbial approach.

Key words: Biofertilizer, biofortification, micronutrients, millets

INTRODUCTION

Micronutrients are crucial and basic elements for wholesome human health and essential for plant development and growth. Among all the micronutrients, iron (Fe) and zinc (Zn) insufficiency in dietetic food are linked with malnourishment signs (also known as 'hidden hunger') which can be corrected through a natural approach known as a biological fortification (Suganya *et al*. 2021). Several stratagems, such as conventional, plant breeding, and molecular approaches or usage of chemical micronutrient fertilizers, have been used to grow fortified crops with improved availability of micronutrients, all these technologies are time-consuming (except chemical inputs) and moreover, not cost-effective (Sindhu *et al*. 2019).

The chief outcomes associated with the micronutrients mobilization by microbes emphasized the implication of

1) rhizospheric soil acidification
2) stimulation of phenolics secretion
3) alterations or changes in root architecture and morphology
4) lessening of phytate in food grains, and
5) Fe/ and Zn transporters upregulation (Singh and Prasanna 2020).

Globally half of the world's population is getting affected by micronutrient malnutrition (also known as hidden hunger), further, the less supply of these vital elements leads to several deficiencies and diseases, illness, which causes increased mortality and morbidity rates (WHO 2002). Many underdeveloped and developing countries are mainly affected by this hidden hunger (Subramanian *et al*. 2009). Humans consuming these essential micronutrients either from plants or animal products, though the soil is the main reservoir and supplier of these nutrients. Decreased micronutrients quantity and bioavailability in the soil have been recorded over the past decades (Singh 2008; Chaudhary *et al.* 2020). The nutritional quality of food plays an important role in human health. Cereals have been focused on micronutrient supply as they are mainly used in the staple diet, although they have a low content of micronutrients (Shukla *et al*. 2014). Millets are the first grain known to be used for human consumption, with rich nutritional and medical values. Millets are an under-used and abandoned crop as people having less knowledge about its benefits but now day's people are much aware of fitness and nutrition-conscious and millets are gaining attention in developing countries also (Singh and Sarita 2016; Singh and Chauhan 2019). Millets are the storehouse of nutrition, helpful in the prevention of several health ailments, therefore, combating hidden hunger (Nithiyanantham *et al*. 2019; Singh and

Chauhan 2019). Millets are divided into two subcategories i.e. large and small millets as mentioned by (Bommy and Maheshwari 2016; Singh and Sarita 2016), illustrated in Fig.1.

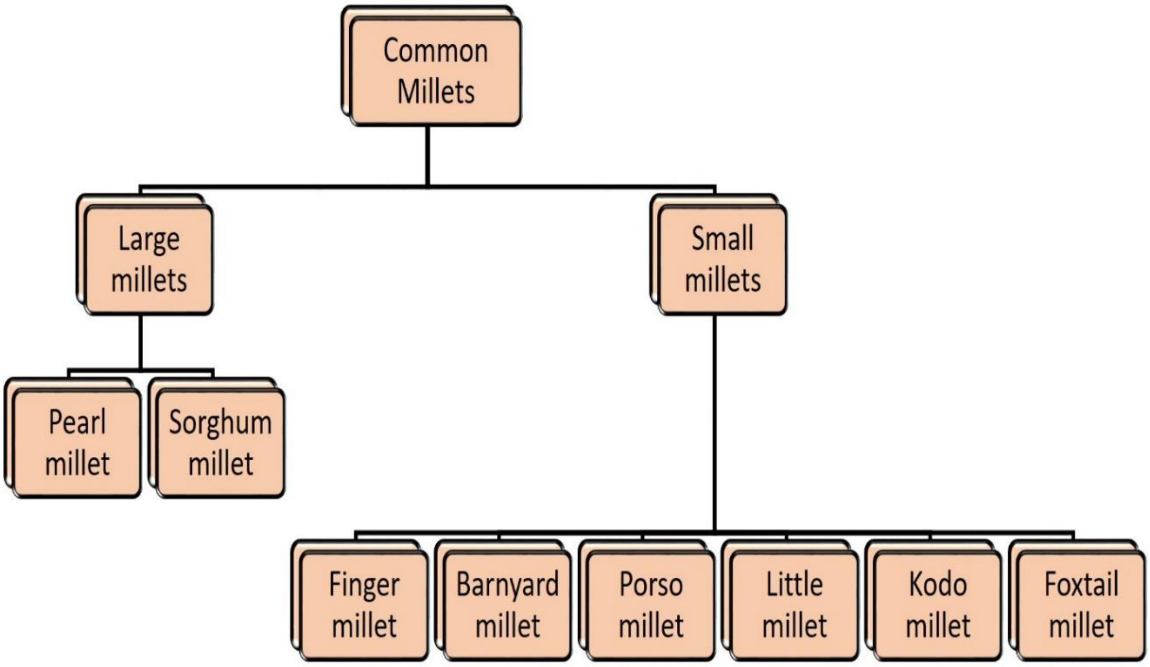

Figure 1. Different types of millet consumed all over the globe

Global distribution and production of millet

According to the report and statistics of FAO (2009), globally 26.7 million metric tons of millets are produced from 33.6 million hectare area. Africa ranked as the top producer with 23.3 million metric tons followed by Asia. The millet production increased during 2014 and sorghum ranked fifth after other major cereals. FAO (2018) reported that India was on the top among the other ten countries in millet production as depicted in Fig. 2.

In India, sorghum and pearl millet are majorly grown crops in several parts of the country such as Andhra Pradesh, Rajasthan, and Maharashtra. The southern and central parts of the country also contribute to small millet production (Rao *et al.* 2017).

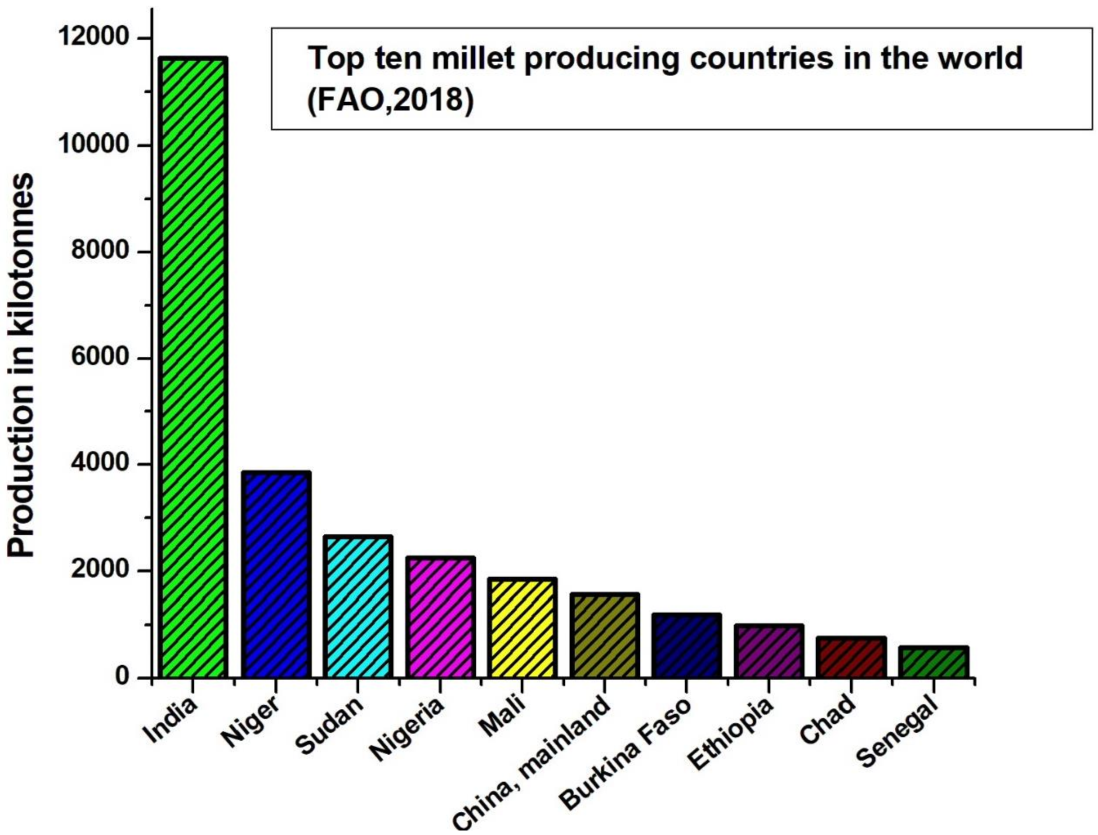

Figure 2. Millet production report of world's top ten countries

NUTRITIONAL COMPOSITION OF MILLETS

Millets are the houses of multi nutrition hence they are consumed as a solution for hidden hunger and are therefore known as 'nutricereal'. Millets are an abundant source of micronutrients, phytochemicals, and significant nutrients such as proteins, minerals, carbohydrates and vitamins, it also includes a high quantity of dietary fiber as compared to wheat and rice (Kumar *et al*. 2018; Abah *et al.* 2020). Millets are also the rich source of amino acids with a relatively high amount of methionine and the least amount of threonine (Ambati and Sucharitha 2019). Some major millets also possess antioxidant properties such as foxtail millet and proso millet, they harbor tocopherols and polyphenolics (Kumar *et al*. 2018). Although all varieties of millets are beneficial for human consumption but they vary at their nutritional level. Table. 1, 2, 3 and 4 describe the average nutrients composition of millets grain.

Table 1. Millet's nutritional composition and dietary fiber (per 100 g)

Minerals	**Sorghum *Sorghum bicolor***	**Pearl millet (*Pennisetum***	**Finger millet (*Eleusine coracana*)**	**Foxtail millet *Setaria italica***	**Kodo millet (*Setaria italica*)**	**Barnyard millet *Echinochloa esculenta***	**Little millet *(Panicum miliare*)**	**Proso millet *Panicum***

		***typhoideum*)**						***miliaceum***
Protein (g)	9.01	10.96	7.16	12.30	8.92	6.20	8.92	12.50
Total fat (g)	1.73	5.43	1.92	4.30	2.55	2.20	2.55	1.10
Dietary fiber (g) total	10.22	11.49	11.18	19.1	6.39	-	6.39	9.0
Dietary fiber (g) insoluble	8.49	9.14	9.51	-	4.29	-	5.45	8.5
Dietary fiber (g) soluble	1.73	2.34	1.67	-	2.11	-	2.27	0.5
Carbohydrates (g)	67.68	61.78	66.82	60.09	66.19	65.55	65.55	70.04
Energy(KJ)	1398	1456	1342	331	1388	307	1449	341

Source: Hulse *et al*. (1980); Ravindran (1992); Gopalan *et al*. (1996); Malleshi and Klopfenstein (1998); Saleh *et al*. (2013); Das *et al* (2019); Rao *et al*. (2017).

Table 2. Trace elements and minerals composition in millet (mg/g)

Minerals	**Sorghum (*Sorghum bicolor*)**	**Pearl millet (*Pennisetum typhoideum*)**	**Finger millet (*Eleusine coracana*)**	**Foxtail millet *Setaria italica***	**Kodo millet (*Setaria italica*)**	**Barnyard millet *Echinochloa esculenta***	**Little millet *(Panicum miliare*)**	**Proso millet *Panicum miliaceum***
Aluminum	2.56	2.21	3.64	-	1.07	-	-	-
Arsenic	1.53	0.97	-	-	-	-	0.49	-
Cadmium	0.002	0.003	0.004	-	-	-	0.001	-
Calcium	27.60	27.35	364	0.01	15.27	-	16.06	-
Chromium	0.010	0.025	0.032	0.030	0.021	0.030	0.016	0.020
Cobalt	0.012	0.030	0.022	-	0.005		0.001	-
Copper	0.45	0.54	0.67	1.40	0.26	1.40	0.34	1.60
Iron	3.95	6.42	4.62	2.8	2.34	15.2	1.26	3.31
Zinc	1.54	2.95	1.5	2.19	-	-	-	1.81

Lead	0.008	0.008	0.005	-	-	-	-	-
Lithium	0.001	0.003	0.003	-	0.027	-	-	-

Source: Hulse *et al.* (1980); Changmei and Dorothy, 2014; Deshpande *et al*. (2015); Kumar *et al.* (2018); Das *et al*. (2019) Renganathan *et al.* 2020; Golpalan *et al.* (1996); Rao *et al.* (2017).

Table 3. Vitamins profile in millets (mg/100 g)

Minerals	**Sorghum (*Sorghum bicolor*)**	**Pearl millet (*Pennisetum typhoideum*)**	**Finger millet (*Eleusine coracana*)**	**Foxtail millet *Setaria italica***	**Kodo millet (*Setaria italica*)**	**Barnyard millet *Echinochloa esculenta***	**Little millet *(Panicum miliare*)**	**Proso millet *Panicum miliaceum***
Thiamine (B1) (mg)	0.35	0.25	0.37	0.59	0.29	0.33	0.26	0.41
Riboflavin (B2) (mg)	0.14	0.20	0.17	0.11	0.20	0.10	0.05	0.28
Niacin (B3) (mg)	2.10	0.86	1.34	3.20	1.49	4.20	1.29	4.50
Pantothenic acid (B5) (mg)	0.27	0.50	0.29	0.82	0.63	-	0.60	1.20
Biotin (B7) (µg)	0.70	0.64	0.88	-	1.49	-	6.03	-

Source: Hulse *et al*. (1980); Leder (2004); Konapur *et al*. (2014); Malleshi and Klopfenstein (1998); Deshpande *et al*. (2015); Kumar *et al*. (2018); Prajapati *et al*. 2019; Golpalan *et al.* (1996)**;** Rao *et al.* (2017).

Table 4. Amino acid constituents in millets (mg/100 g of protein)

Amino acids	**Sorghum (*Sorghum bicolor*)**	**Pearl millet (*Pennisetum typhoideum*)**	**Finger millet (*Eleusine coracana*)**	**Kodo millet (*Setaria italica*)**	**Little millet *(Panicum miliare*)**
Histidine	2.07	2.15	2.37	2.14	2.35

Isoleucine	3.45	3.45	3.70	4.55	4.14
Leucine	12.03	8.52	8.86	11.96	8.08
Lysine	2.31	3.19	2.83	1.42	2.42
Methionine	1.52	2.11	2.74	2.69	2.21
Cystine	1.06	1.23	1.48	1.92	1.85
Phenylalanine	5.10	4.82	5.70	6.27	6.14
Threonine	2.96	3.55	3.84	3.89	4.24
Tryptophan	1.03	1.33	0.91	1.32	1.35
Valine	4.51	4.79	5.65	5.49	5.31

Source: Hulse *et al*. (1980); Ravindran (1992); Devi *et al*. (2011); Bagdi *et al*. (2011); Kamara *et al.* (2009); Malleshi and Klopfenstein (1998); Golpalan *et al*. (1996); Prajapati *et al*. (2019); Rao *et al*. (2017); Ejeta *et al*. (1987).

NUTRACEUTICAL BENEFIT OF MILLETS

According to Global Nutritional Report data, 2016 collected from 129 countries, about 44 % population is affected by serious health issues such as obesity, heart disorders, diabetes, and malnutrition. In a report from FAO (2015), poor nutrition and an imbalanced diet are the common cause of hidden hunger and many health disorders. Millet grains harbor many essential nutritional elements which can combat hidden hunger and their consumption helps in disease-fighting as they are rich in nutrients (Gupta *et al.* 2012; Kumar *et al.* 2018).

Regular consumption of millets provides the disease-fighting ability and improves nutrition imbalance. According to a study, millets have the potential to decrease blood glucose levels. It is also helpful in the elimination of cardiovascular risk, celiac disease, obesity, and cancer (Devi et al. 2011; Singh and Raghuvanshi 2012; Rao *et al.* 2017; Kumar *et al*. 2018; Nithiyanantham *et al*. 2019; Ramashia *et al.* 2019; Singh and Chauhan 2019). Various health-related beneficial properties of millets are mentioned in Fig. 3

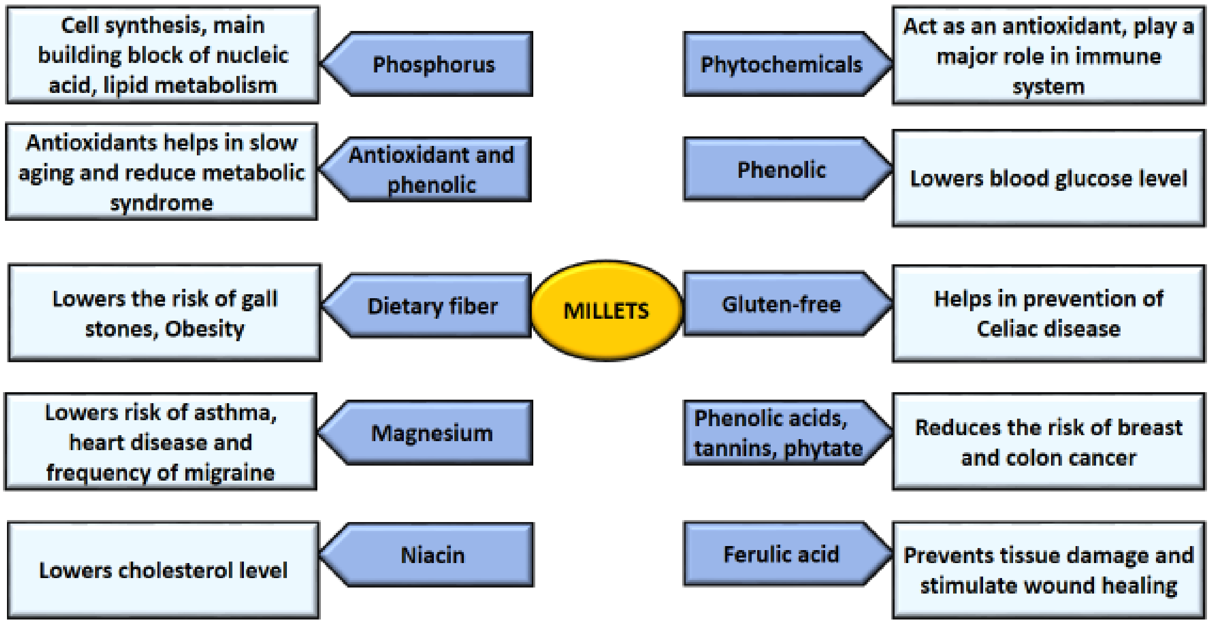

Figure 3. Nutraceutical properties of millets [Source: Amadou *et al.* (2013); Changmei and Dorothy (2014); Kumar *et al.* (2018), Nithiyanantham *et al*. (2019)].

Since the grains of millets are the great source of many micronutrients and the millet crops accumulate these vital elements from soil, but it has been observed that millets suffer from one or more than one micronutrient deficiency even though adequate nutrients are present in the soil. The deficiency of these micronutrients may also depend upon the crop type, soil type, and plant genotype or agro-ecological conditions (Singh 2008). Another reason could be the plant root's inefficiency in up taking and mobilizing micronutrients to the grains (Chaudhary et al. 2020).

Micronutrient deficiency has become the major challenge and is a concern for sustainable and nutritious crop production in the world, which is one of the main reasons behind malnutrition and several health issues in human beings (Amadou *et al.* 2013; Chandra *et al*. 2016). In many investigations, zinc and iron deficiency were ranked highest among all micronutrients. Although several approaches have been exploited for the fortification of micronutrients yet their acquisition varies from crop to crop (Singh *et al.* 2010). Chemical fertilizers are being used to improve the status of nutrients in the soil, but in many types of research, their negative impact has been recorded on the crop, soil equilibrium and also, they harm the living organisms in habitat and human being (Singh and Prasanna 2020), (Kaur *et al*. 2020).

Role of micronutrients

Micronutrients play a significant role in the growth, development, and health of humans and plants. Human acquires these essential micronutrients from plants, their deficiency impairs metabolism, cellular function, reproduction and growth in humans (Nithiyanantham *et al*. 2019; Singh and Chauhan 2019) and also negatively influences the crop plants (Graham 2008; Narwal et al. 2017). The world's nearly 3 billion population suffers from micronutrients deficiency (Goswami *et al.* 2016). Micronutrients are very essential, but they are required in small quantities for the overall plant growth and development, they are vital for essential enzyme reactions of respiration and photosynthesis (Hänsch and Mendel 2009). They are also essential for soil health and improved crop productivity. Each micronutrient has different functions and their required quantity varies depending upon the type of crop and their requirement (Grusak 2001; Rattan *et al.* 2009). The primary source of these micronutrients is agriculture, the crop requires 17 macro and micro-nutrients (C, H, N, K, Ca, S, O, Cu, Mg, Mn, Fe Zn, P, Mo, Cl, Ni, and B) for their development (Goswami *et al*. 2016; Narwal *et al.* 2017).

Iron, zinc, copper, boron, and manganese play a key role in the overall growth and metabolic functions of plants. Micronutrients are involved in the biosynthesis of nucleic acid, amino acids, expression of genes, phytohormones, lipids and carbohydrate metabolism, production of secondary metabolites, chlorophyll synthesis, stress tolerance, etc. (Jatav *et al.* 2020).

Deficiency of micronutrients (iron and zinc) in soil: reasons

Various ecological, microclimatic and biological, physical, and chemical factors of soil, (Ibrahim *et al.* 2011; Rengel 2015). Further, the bioavailability of micronutrients is also affected in soils that are more likely to waterlogging conditions, or soils having peat or calcareous characteristics (Steffens *et al*. 2005; Gul *et al.* 2013; Dhaliwal *et al.* 2019).

A maximum proportion of iron on the earth's crust exists as a ferric ion (Fe^{3+}) which is not effortlessly available to plants. The ferrous ion form (Fe^{2+}) is a more soluble form of iron, but it quickly oxidized to the ferric form (Fe^{3+}), which got precipitated into carbonate, hydroxide/oxide, phosphate, and other inaccessible intricate forms in soils (Lindsay and Schwab 1982; Jones *et al.* 2014). Though in soils, there is a huge quantity of iron is present, but the bioavailability of this vital nutrient is very little. It has been suggested that bioavailability of Zn is also reduced in soil, with increased in soil pH owing to the adsorption or precipitation of zinc on the surface of Fe oxides and $CaCO_3$ (Chirwa and Yerokun 2012; Rutkowska *et al.* 2015), (Sidhu and Sharma (2010), (EC) (Chattopadhyay *et al.* 1996). Gao *et al* (2011).

Importance of micronutrients (iron and zinc) and their health implications

- ***Zinc:*** Zinc is an essential component for plants and human health, in plants, (Palmer and Guerinot 2009; Sharma *et al.* 2013). Zn is also helpful in the process of cell proliferation, differentiation, and chloroplast development (Palmer and Guerinot 2009; Sharma *et al.* 2013).

Regions having zinc-deficient soils also show widespread zinc deficiency in humans (Barman *et al.* 2018). Zinc deficiency adversely affects plant growth, chloroplast synthesis, and tolerance to various stresses (Lee *et al.* 2012). In the deficiency of zinc, there is a shortening of internodes, yellow coloration at the growing point of root and shoot with dwarfing, rusting in older leaves, size of the leaf is also reduced, the vascular bundle becomes silver white (Mattiello *et al.* 2015), (Tapiero and Tew 2003). It is an essential micronutrient required for overall growth and development in humans, since Zn ion plays a vital role in reproductive health, neurological and sensory functioning (Herschfinkel *et al.* 2007). Deficiency of zinc leads to oligospermia, neurological disorders, immune system disfunctioning and hyperammonemia (Prasad 2008; 2013).

- ***Iron:*** Iron is one of the essential micronutrients that plays a major role in all living organisms and plant growth, it has the potential to reverse the chlorosis in the plant. Iron-containing protein such as cytochrome contains iron which participates in the electron transport system in chloroplast and mitochondria in the plant (Schmidt et al. 2020). Certain non-iron-containing proteins also contain iron such as ferredoxin (Hochmuth 2011). Iron plays an essential role in the formation of chloroplast structure and functioning, respiration, nitrogen fixation, DNA synthesis, protection from ROS, repair, and control of cell cycle and also participate as a co-factor for many enzymatic reactions in phytohormones production (Siedow 1991; Bertini and Rosato 2007). The imbalance in Fe in the soil leads to the deficiency of iron in plants which causes yellow coloration of young leaves and the veins of the leaves remain green (Morrissey and Guerinot, 2009). It affects mainly the younger leaves as there is low mobility of iron. The bioavailability of iron is low because of its insoluble form (ferric) present in the soil (Rout and Sahoo 2015). Iron is a necessary mineral required for red blood cells production and redox reactions. The deficiency of iron leads to poor health, shortness of breathing, tiredness, anemia, impaired physical activity, and learning disorders in children and also in adults. Women and children are more affected by iron deficiency due to malnutrition (Abbaspour *et al*. 2014). Now a day's iron deficiency anemia has become a major health issue, since one of the main reasons is that people are consuming plants and their products from iron-deficient soils (Martınez-Navarrete *et al*. 2002).

Biofertilization

At present time, eco-friendly agriculture has become very challenging. Fertilizers are an integral part of good crop production and their use can also reduce the amount of nutritional losses in the soil, but according to many pieces of research, it has been investigated that intensive and injudicious application of chemical fertilizer not only damages the crop and its production but also the soil environment (Dong *et al.* 2012; Sharma *et al*. 2014; Patra *et al.* 2016; Iqbal *et al*. 2021), (Iqbal *et al.* 2021). To overcome this problem, microbial inoculants could be an effective initiative to improve agriculture and to avoid the crop from ill effects of agile fertilizers (Alori and Babalola 2018; Kumar *et al.* 2018). These microbial inoculants are named biofertilizer, which consists of living cell consortium (bacteria or fungi), (Ahmad *et al*. 2018).

The live or dormant microbial consortia applied as biofertilizer have the efficiency to solubilize phosphate, iron and zinc, fixes nitrogen, and promotes plant growth parameters. Although they do not come up with nutrients, they are the link in the acquisition of micronutrients and minerals from the soil to the plant (Sahai and Kumar 2017), (Berruti *et al.* 2015; Khatri *et al*. 2016; Ribeiro et al. 2018. These microbial inoculants not only improved the nutrients accessibility to the plant but were also helpful in the management of disease and control of pests and weeds (Khatri *et al*. 2016). According to many studies, these microbial consortium produces secondary metabolites which accelerate the plant growth-promoting attributes and results in healthy plant growth (Alori and Babalola 2018). Application of biofertilizer shows a significant beneficial effect on crop yield, which may vary and depends upon the different crop type, climate, soil diversity, and nutrient composition of rhizospheric soil (Schütz *et al*. 2018). Biofertilizers or plant growth-promoting microorganisms promote plant growth and enhance the nutrient bioavailability via many processes such as oxidation-reduction, metal chelation, solubilization, etc. during these processes the root exudate from the crop also helpful in balancing soil pH, and improves soil quality and structure (Kaur *et al*. 2020).

Potential microbes employed biofertilizers, also can meet the deficiency of zinc and iron micronutrients found in soil. For solubilization and mobilization of iron and zinc in soils, microbes produce siderophores, which are low molecular weight proteinaceous compounds, which chelate these metals (Chaudhary *et al.* 2020). Microbes secrete different organic acids, produce essential signaling molecules such as proton extrusion and phytohormones, reduce the amount of phytic acids in the grain, and increase the stimulation of iron and zinc transporters (Kaur *et al*. 2020; Singh and Prasanna 2020). In the process of biofortification, both plant growth-promoting rhizobacteria i.e. rhizospheric and endophytic microorganisms play a significant role in the acquisition of zinc, iron, and other micronutrients. In this regard, endophytic microbes (fungal and bacterial) are more reliable in the solubilization and accumulation of micronutrients, since they influence the metal transportation process of the host plant and enhance their uptake. (Reiter *et al.* 2002; Gosal *et al*. 2010; Sharma *et al.* 2012; Singh and Prasanna 2020). Rhizospheric microbes colonize and remain attached to the plant surface while endophytic microorganisms colonize inside the host plant tissue especially in the apoplastic region, although some endophytic organisms may also found inside the intracellular regions of root, stem, leaves, seed, etc. The exploitation of beneficial microbes in agronomic biofortification is accomplished by several methods such as seed priming, root inoculation, foliar spray, and soil incorporation resulted in enhanced yield in staple crops (including millet) (Khatri *et al*. 2016; Kumar *et al.* 2020). In many studies, it has been mentioned that the fertilizer application along with bioinoculants resulted in improved plant micronutrients such as zinc, iron and also improved the soil physical, biological and chemical properties (Shi *et al.* 2010; Kutman *et al.* 2011; De Valença *et al.* 2017; Singh and Prasanna 2020). One study conducted by Ribeiro *et al.* (2018) reported the potential of endophytic bacteria in micronutrient mobilization, four *Bacillus* strains were inoculated to pearl millet and evaluated plant growth promoting attributes. All *Bacillus* strains exhibited plant growth-promoting attributes while three of them (strain B1923, B2084, and B2088) produced siderophores, solubilized, and mobilized iron-phosphate. Another study conducted by (Tewari *et al.* 1993) reported that fungal endophytes are very beneficial in the accumulation of micronutrients. Fungal endophytes (*Glomus caledonicum, Gl. mosseae, Gl. fasciculatum, Gl. epigaeum, Gigaspora calospora, G. margarita*) mobilized micronutrients (Zn, Fe, Cu, and Mn) when inoculated into finger millet plant. Inoculation of these endophytic fungi also demonstrated plant growth-promoting attributes, resulting in better millet plant growth and root biomass. Rhizobacterial (*Bacillus* sp. and *Rhizobium* sp.) potential to enhance the nutritional level and productivity in foxtail millet (*Setaria italica*) has been reported by Khatri et al (2016). The aspects of plant growth-promoting bioinoculants have been illustrated in Fig 4.

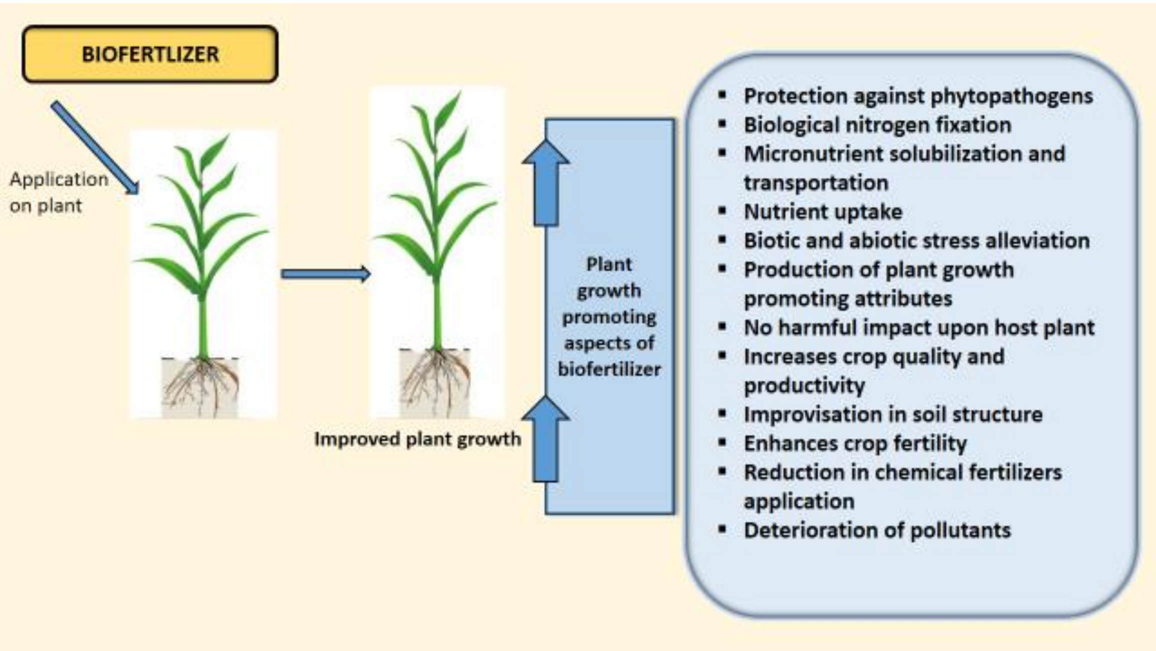

Figure 4. Plant growth promotional attributes of a bioinoculant.

Endophytes in Iron and zinc uptake

Microorganisms have been playing a significant role in the growth of millet plants for the last few decades, bacterial endophytes reported as a beneficial agent in micronutrient solubilization and transport to the plant (Kushwaha *et al.* 2019; Sindhu *et al.* 2019). There is not so much literature available on the biofortification of millets, since people carried out more work on popular cereal's biofortification.

- ***Fe uptake:*** Bacterial endophytes have the capability to solubilize and transport micronutrients to the host plant. They perform the process of iron mobilization either by direct or indirect mechanisms and convert iron from unavailable to available form. Bacterial endophytes help in the accumulation of iron by producing iron-chelating compounds siderophore. The Finger millet plant harbors a variety of endophytes. Kumar *et al* (2020) isolated bacterial endophytes *Paenibacillus dendritiformis*, *Enterobacter cloacae*, and *Enterobacter hormaechei* from finger millet seeds. Among these strains, *Paenibacillus dendritiformis* and *Enterobacter hormaechei* produced siderophore and other phytohormones. In another similar study, four *Bacillus* endophytic strains were isolated from pearl millet plant were examined for iron-phosphate solubilization, and according to the report (Ribeiro *et al.* 2018). Reddy *et al.* (2019) isolated twelve endophytic bacteria from foxtail millet and all the strains produced siderophore and they also solubilized and transported iron from soil to the host plant.
- ***Zn uptake:*** In a study, several bacterial endophytic strains belong to the phylum Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria have been reported as potential zinc solubilizers and these isolates increased the availability of zinc for millet plant and effectively solubilized insoluble form of zinc. These potential microbes also promote plant growth by producing ammonia, IAA, hydrogen cyanide, siderophore, nitrogen fixation, etc. In another study, nutrient solubilization potential of endophytic bacteria isolated from pearl millet has been reported. Endophytic strains were identified as *Bacillus aryabhattai B. pacificus, B. halotolerans, B. subtilis, B. wiedmannii, B. tequilensis, Bacillus safensis, B. amyloliquefaciens, B. haynesii, B. proteolyticus, B. albus, B. paramycoides, Bacillus altitudinis, and Bacillus cereus.* These bacterial isolates exhibited noticeable zinc solubilization by producing a clear halo zone around the colonies (Kushwaha *et al.* 2019). On the same lines, Kushwaha et al (2020) isolated bacterial endophytes from pearl millet, identified as *Bacillus subtilis subtilis*, *Bacillus amyloliquefaciens*, and *Bacillus cereus* exhibited micronutrient mobilizing property, isolates solubilized zinc, phosphate, and potassium.

Mechanism of Iron and zinc biofortification

To improve the bioavailability of Zn in soil, the Zn-solubilizing microbes employs several actions of mechanisms (Kamran *et al.* 2017). Generally, the common mechanism involve in unlocking several micro nutrients in the soil and rhizospheric region is the pH reduction. It has been reported that, decrease in one-unit in soil pH can improve hundred times Zn availability (Mumtaz *et al.* 2017). Potential microbes releases the organic acids, these acids provides both organic ion and protons, which function as chelating agents in the rhizospheric zone (Kamran *et al.* 2017). Possibly other processes implicated in zinc solubilization involve siderophores production (Saravanan *et al.* 2011) and protons, oxido-reductive systems on chelating ligands and cell membranes. It is essential to state that zinc solubilizing microbes does not depend on one approach to solubilise the trace metals, rather depending on the situation, the mechanism exercised changes. For instance, glucose as carbon source in the cultural broth encouraged production of organic acids (oxalic, gluconic and malonic) by zinc solubilizing bacteria (Goteti *et al*. 2013), resulting in medium acidification and leading to solubilization of subsequent ZnO. On the other hand, in glucose absence, dissolution of ZnO resulted from extrusion of protons (Costerousse *et al.* 2017). Organic acids are not only excreted by rhizospheric bacteria, but some soil AM fungi are also reported to produce organics, which solubilizes zinc phosphate in the rhizospheric zone (Rashid *et al.* 2016). A decline in rhizospheric soil pH after inoculation of AM fungi resulted in zinc release from the soil mineral section (Begum *et al.* 2019; Suganya *et al.* 2021). Though, the scale of soil pH reduction is subjected to numerous reasons such as soil type and texture, topographical location, and soil associated microbiome. Besides lowering the pH, soil microbes also carry out other role to mobilize the zinc metal to the plant parts. Production of zinc binding compounds too have the capability to improve bioavailability of zinc in the rhizospheric zone, which is finally captivated by the roots and shipped to the plant parts (Goteti *et al.* 2013; Kamran *et al.* 2017). Several zinc solubilizing bacteria, such as *Pantoea agglomerans, Pantoea dispersa, Pseudomonas* sp., *Rhizobium* sp., and *E. cloacae* to make chelating metallophores which upsurge water soluble zinc concentration in the rhizospheric soil for plants uptake (Kamran *et al.* 2017). A biostimulant consortium having *Azospirillum lipoferum*, *Pseudomonas* sp., and *Agrobacterium* sp. enhanced bioavailability of zinc for prolonged duration in the soil by liberating ethylene diamine tetra acetic acid (EDTA) as main chelating agent (Tariq *et al.* 2007). Since zinc being an immovable soil element and increasing the surface area of roots might be alternative approach to enhance zinc availability. To achieve this, AM fungi association with roots can augment the root surface area, aiding plants to take up more zinc from the adjacent soil (Deeksha and Sachan 2017). Inoculation of AM fungi resulted in enhancement of 4% more Zn in grains as compared to non-inoculated plants (Subramanian *et al.* 2009). Under iron limiting conditions, there are explicit organic compounds having low molecular weight (1-2 kDa) made by rhizospheric as well as endophytic bacteria, known as microbial siderophores (Etesami and Beattie, 2017; Lurthy *et al.* 2020). These organic compounds can chelate at high specificity Fe^{3+} ions, thus increasing solubility of iron. When this Fe-siderophore complex attaches to particular bacterial receptors, iron is simply absorbed and transformed to Fe^{2+} (Radzki *et al.* 2013; Eid *et al*. 2019). These siderophores are categorized into three groups: hydroxamates, catecholates (phenolates), and carboxylates, this is as per to the ligands that attach to Fe^{3+} (Hider *et al*. 2010; Ansari *et al*. 2017).

Gram-positive and negative bacteria are able to produce siderophores under iron insufficiency (Rajkumar *et al.* 2010; Kumar 2019). The iron binding compounds are manufactured by numerous bacteria for instance, *Aeromonas, Agrobacterium, Bacillus, Burkholderia, Citrobacter, Enterobacter, Escherichia, Flavobacterium, Klebsiella, Pseudomonas fluorescens, Rhizobium,* and *Stenotrophomonas*, *Streptococcus, Vibrio* (Gram *et al.* 2001; García *et al*. 2012; Retamales *et al.* 2012; Kannahi and Senbagam 2014; Sepehri and Khatabi 2021).

In dicots and monocots (non poaceae) plants, strategy I is used for iron uptake, it is a reduction based iron acquisition mechanism (Marschner and Römheld 1994; Kim and Guerinot 2007). This approach comprises three stages for iron uptake: 1. exudation of protons to increase iron movement, 2. reduction of ferric ion (Fe^{3+}) to ferrous ion (Fe^{2+}) and 3. import of ferrous (Fe^{2+}) into the roots.

Plant having strategy II, the plant-siderophore fastened Fe^{3+} ion could be right away transported into the roots by precise plant transporters without reducing the iron metal (Kim and Guerinot 2007. In addition to these plant-siderophores, soil microorganisms also manufacture and excrete iron binding siderophores (Neilands and Leong 1986; Briat 1992) which are suggested to ease the uptake and mobility of soil iron by plant roots (Colombo *et al.* 2014; Schmidt and Buckhout 2020). Figure 5 shows the common mechanism employed by microbes to mobilize zinc and iron to the sink.

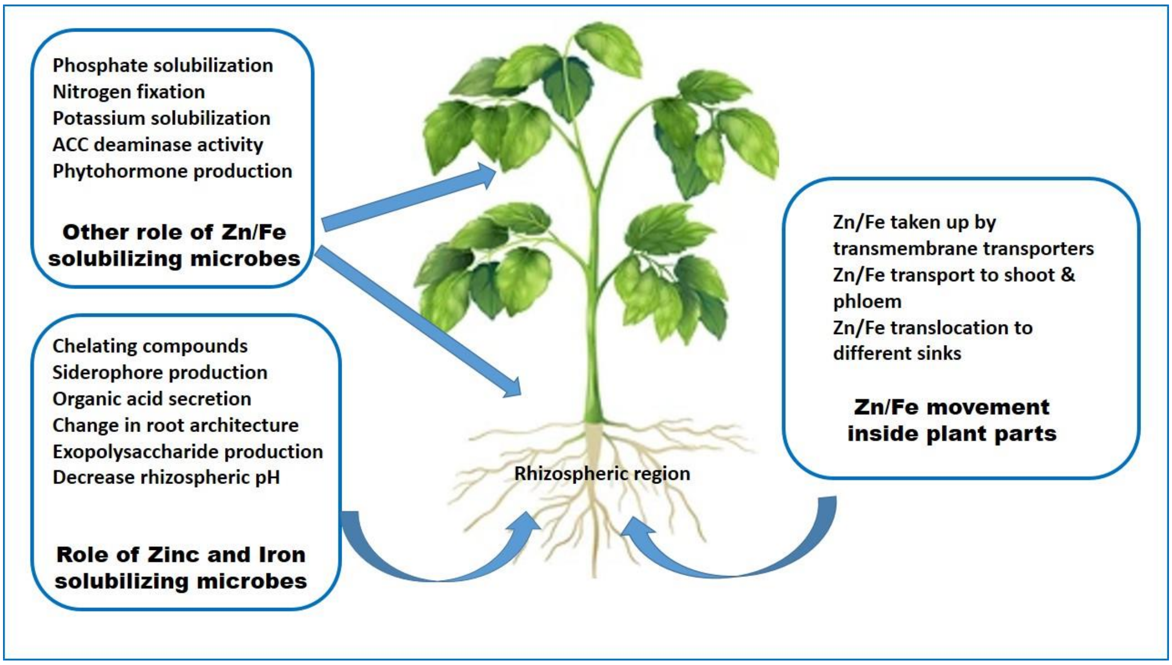

Figure 5. Mechanism employed by microbes to mobilize Zn/Fe into the plant

CONCLUSIONS

The accessibility of fewer quantities of micronutrients is commonly recognized as "hidden hunger" and attracts less importance than the noticeable individual's malnourishment. As biologists, we need to apprehend, that there is a convoluted interaction between plants, microbes, and soil that is accountable for soil fertility and crop productivity. Henceforth, along with agronomic and plant breeding fortification, substantial exertions are required to include potential microbes as beneficial associates in such practices. Forthcoming biofortification issues include combined efforts of know-hows toward delivering nourishing and healthy food for the ever-growing population, employing viable, feasible, and eco-friendly approaches. For biological fortification of Fe and Zn, formulation(s) of competent microbiomes can be searched as soil dressing or seed priming possibilities. Employing contemporary transcriptomics and genomics, the proteins/genes intricate in micronutrient mobilization within the millets can be recognized and persuaded to improve the efficiency of plant-microbes synergism.

Millets are great healthy and nutritive crops feeding deprived inhabitants in Africa and Asia. Systematic research to exploit the very nutritive millet crops to fight micronutrients malnourishment is still insufficient. In good quality millet grains, considerable quantities of minerals, vitamins, and essential amino acids, the bioavailability of micronutrients needs further enhancement by reducing anti-nutrients such as phytic acid or by using unique promoters. Moreover, microbial precise role in changing millet's root morphology and upregulation of genes for iron and zinc uptake needs to be deciphered for enhanced mobilization.

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