



IMPROVING THE ZINC-USE EFFICIENCY IN PLANTS: A REVIEW

T.P. AJEESH KRISHNA¹, S. ANTONY CEASAR^{1,2}, T. MAHARAJAN¹,
M. RAMAKRISHNAN¹, V. DURAIPANDIYAN^{1,3}, N.A. AL-DHABI³ and
S. IGNACIMUTHU^{1*}

¹Division of Plant Molecular Biology, Entomology Research Institute, Loyola College, Chennai, 600 034, India

²Centre for Plant Sciences and School of Molecular and Cellular Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, United Kingdom

³Addiriyah Chair for Environmental Studies, Department of Botany and Microbiology, College of Science, King Saud University, P.O. Box.2455, Riyadh-11451, Kingdom of Saudi Arabia

*Corresponding author's email: eriloyola@hotmail.com

Email addresses of co-authors: ajeeshkrishnatp@gmail.com, antony_sm2003@yahoo.co.in, susirajan143@gmail.com, ramkyeri@gmail.com, avpandiyan@gmail.com, naldhabi@ksu.edu.sa

SUMMARY

Zinc (Zn) deficiency causes large scale yield losses in major crops such as rice, wheat and maize. Zn is an important micronutrient and the only metal ion acting as a co-factor for all six classes of enzymes in plants and other organisms. In this review, we have identified the phenotypic and biochemical changes associated with Zn deficiency in plants. We also present the current understanding on uptake and translocation of Zn and provide details on various approaches made to improve Zn-use efficiency (ZUE) in plants. The details of membrane transporters involved in acquisition of Zn from soil and its translocation in plants have been explained. Molecular markers and transgenic tools have been used for improving ZUE in various plants. Over expression of various Zn transporters through transgenic modification improved the Zn uptake in deficient Zn condition. Several quantitative trait loci (QTL) related to Zn content in rice grain have been identified. Further studies based on molecular markers and functional genomics will help improve ZUE and yield in crop plants grown in low Zn soil.

Key words: Zinc, zinc deficiency, zinc transporters, zinc-use efficiency, molecular markers.

Key findings: In this review, we present the Zn-plant relationship, mechanism of Zn transport in plants and efforts made so far to improve Zn-use efficiency in plants using various complementary approaches.

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INTRODUCTION

Plants are irreplaceable resources of foods that provide energy and nutrients to both humans and animals. Plants need various nutrients in different amounts for their development and reproduction. In agriculture, nutrients are essential for growth and yield of crop plants (Sadeghzadeh, 2013). These nutrients play major

roles in physiological and metabolic activities of plants. Unavailability of one or more of these elements prevents plants from completing their life cycle (Ramesh *et al.*, 2004).

Zinc (Zn) interacts with both the macro and other micro-nutrients that are involved in many physiological functions of plants (Brar and Sekhon, 1976; Slamet-Loedin *et al.*, 2015). Zn is an important micronutrient for cellular

metabolism and biological activities such as anti-oxidative defense, carbohydrate metabolism, protein synthesis and auxin metabolism (Broadley *et al.*, 2007). Zn also plays a crucial role in enzyme activity; it is the only element necessary to activate all six classes of enzymes (oxidoreductases, transferases, hydrolases, lyases, isomerases and ligases) (Sadeghzadeh, 2013). More importantly Zn is an essential co-factor for approximately 300 individual enzymes in plants (Rathore and Mohit, 2013).

Plants require low concentration of Zn (0.5 to 2 μ M) from the soil (based on our unpublished study). Both lower and higher quantities of Zn cause adverse effects to plants. The Food and Agriculture Organization (FAO) reported that 50% of the world's agricultural soil is low in Zn (Das and Green, 2013). Zn deficiency occurs in many crop species such as *Oryza sativa* (rice), *Sorghum bicolor* (sorghum), *Zea mays* (maize), *Hordeum vulgare* (barley) and *Arachis hypogaea* (peanut). Low availability of Zn also significantly affected the nutritional quality and yield in *Triticum aestivum* (wheat) (Cakmak *et al.*, 1996). Rice, sorghum and maize are categorized as highly sensitive to Zn deficiency, and barley, wheat, *Avena sativa* (oat) and *Secale cereale* (rye) as less sensitive (Viets Jr *et al.*, 1954; Clark *et al.*, 1990).

Zn-use efficiency (ZUE) has been defined as the efficient acquisition of Zn and utilization or (re)-translocation within a plant in Zn deficient condition (Graham and Rengel, 1993; Erenoglu *et al.*, 2000). Certain genotypes are able to grow and yield well under Zn deficiency, which has been termed Zn efficiency (Graham and Rengel, 1993). This may be due to some genetic variations present in plants. Only limited information is available on the genetic control of Zn efficiency mechanisms, its molecular backgrounds and genes responsible for Zn efficiency (Sadeghzadeh, 2013). The physiological mechanisms involved in Zn efficiency have been documented by many researchers (Hacisalihoglu and Kochian 2003). In this review, we present the details on Zn deficiency in crop plants, phenotypic and genotypic differences, biochemical changes, agronomic aspects of managing low Zn in soil.

Apart from this, we also cover Zn transport and efforts to improve ZUE in various plants.

Zn status in relation to water status

In soil, Zn solubility and availability to plants varies between water logged soil and dry land soil (Gao *et al.*, 2012). Zn deficiency symptoms are more noticeable in plants grown under dry land soils as compared to flooded soils (Huaqi *et al.*, 2002). It is evident that the Zn bioavailability was lower in dry land soils as compared to flooded rice cultivation systems, as indicated by decreased Zn concentration not only in plant tissue but also in Zn uptake and Zn harvest index (Gao *et al.*, 2006). The bioavailability of Zn in soil is controlled by both absorption-desorption reactions and solubility relation (Gao *et al.*, 2012). And the soil solution and solid phase are mainly involved in the absorption-desorption and dissolution-precipitation reactions of Zn in soil. The factors such as organic matter, soil texture, soil pH, redox potential, pedogenic oxide and sulfur contents affect the amount of Zn dissolved in soil (Alloway 2009; Mandal *et al.*, 2000). Aerobic rice cultivation may increase soil pH, leading to reduction in Zn availability than anaerobic condition (Gao *et al.*, 2006). The status of Zn in relation to anaerobic (flooded condition) and aerobic (dry land condition) soil has been recorded by many researchers (Gao *et al.*, 2006; Gao *et al.*, 2012). The reduction of the soil moisture content significantly restricts the transport of Zn towards the plant root (Yoshida, 1981).

Zn deficiency symptoms in crop plants

Hacisalihoglu *et al.* (2001) defined Zn deficiency as the condition in which only insufficient Zn is available for the optimal growth that may cause dramatic reductions in crop yield. The low organic matter, high level of P, calcareous soils, low temperature, and repeated application of N fertilizer can cause Zn deficiency (Bogdanovic *et al.*, 1999; Lindsay, 1972; Mousavi *et al.*, 2012). Plants generally show morphological changes in response to nutrient deficiency. Details on various symptoms associated with Zn deficiency in some plants are

listed in Table 1. Several studies have been performed in crop plants to assess the phenotypic responses to Zn deficiency (Hafeez *et al.*, 2013). Zn deficient plants show stunted growth, delayed fruit maturity, chlorosis, shortened internodes and petioles and malformed leaves (Das and Green, 2013; Hafeez *et al.*, 2013). In rice, Zn deficiency caused seedling mortality, stunted growth, leaf bronzing, and delayed flowering (Widodo *et al.*, 2010). Similarly, wheat showed brown spots on upper leaves under Zn deficiency; chlorosis was seen on the midrib and base of the younger leaves. Other symptoms in wheat included loss of leaves, decreased tillering ability, inhibited growth of shoot and root and more spikelet sterility (Cakmak *et al.*, 1997b). Zn deficiency also affected proper formation of panicles in some cereal crops (Alloway, 2004). We also observed that Zn deficiency affected panicle formation, grain setting and other parameters in sorghum (Figure 1).

Phenotypic studies

Assessment of genotypes in deficient Zn for phenotypic variation may be helpful for choosing genotypes for further breeding works. Several studies have been performed in major crop plants such as rice and barley to assess their phenotypic variation due to Zn stress (Genc *et al.*, 2007; Nanda and Wissuwa, 2016; Sharifianpour *et al.*, 2014). Changes in root architecture have also played essential role in capturing Zn during deficiency. The low availability of Zn significantly affected the root architecture (Fageria, 2004). Induction of longer root types viz. nodal, primary, and lateral roots with less induction of adventitious roots has been found in barley in Zn deficiency (Genc *et al.*, 2007). Early formation of crown roots was affected by Zn deficiency in a Zn-inefficient genotype than in Zn-efficient genotype of rice (Nanda and Wissuwa, 2016). In *Arabidopsis*, Zn deficiency reduced the length of primary root and increased the number and length of lateral roots (Jain *et al.*, 2013). The importance of root traits associated with P and Zn uptake has been highlighted (reviewed in Rose *et al.*, 2013).

The genotypes with better ZUE are believed to utilize Zn more efficiently. For

example, the Zn-efficient genotypes of rice have the ability to translocate Zn from older to actively growing younger tissue compared to Zn-inefficient genotypes (Impa *et al.*, 2013). However, contradictorily, such relation between Zn re-translocation and Zn efficiency does not exist in bread and durum wheat genotypes (Erenoglu *et al.*, 2002). Wissuwa *et al.* (2008) found that the grain Zn concentration was also dependent on the genotype in rice. Zn-efficient genotypes were characterized by higher Zn uptake efficiency in low Zn soil which helps gain higher biomass and yield (Wissuwa *et al.*, 2006). The grain yield efficiency index (GYEI) was also used to sort the genotypes into Zn-efficient and inefficient, in rice (Hafeez *et al.*, 2010). Kumar (2001) studied GYEI in ten lowland rice genotypes for ZUE. These studies are helpful to identify the best performing genotype with efficient ZUE based on GYEI in rice. Similar studies in other crop plants will help find efficient genotypes from the germplasm collection which can be grown in low Zn. Efforts need to be initiated for such studies in other crop species too.

Plant biomass was also used as a crucial diagnostic tool for determining the ZUE in some plants. Zn-inefficient rice genotypes produced less biomass compared to Zn-efficient genotypes (Hoffland *et al.*, 2006; Gao *et al.*, 2009; Widodo *et al.*, 2010). Similarly, Gao *et al.* (2005) grew 23 genotypes of rice in low Zn soil. Zn content and dry matter of seed, root and shoot were taken for the characterization of the genotypes. Several genotypes of oilseed rape (*Brassica napus* and *B. juncea*) (Grewal *et al.*, 1997) and *Arabica coffee* (coffee) (Pedrosa *et al.*, 2013) were screened to find the best performing genotypes in Zn deficient condition based on biomass production. Genotypic responses to Zn deficiency were also demonstrated in field growth experiments in rice. Two rice genotypes (IR55179 and KP) were grown in Zn deficient condition and IR55179 accumulated higher Zn in grain than KP (Impa and Johnson-Beebout, 2012). These basic studies may be helpful to choose the genotypes for use in further studies like marker assisted selection and breeding to produce new varieties with improved ZUE.

Table 1. Details of various diagnostic symptoms of Zn deficiency in important crop plans.

Name of the species	Zn deficiency symptoms	Reference
<i>Hordeum vulgare</i>	Leaves show uniform chlorosis and drying, appearance of white spots on leaves, collapsed mid-leaf and decreased tip growth.	Singh <i>et al.</i> (2005)
<i>Triticum aestivum</i>	Brown spots on upper leaves, midrib becomes chlorotic, mostly seen in leaf base of younger leaves, loss of leaves and lower leaves have brown blotches and streaks appear, decreased tillering, inhibited growth of shoot and root, spikelet sterility.	Singh <i>et al.</i> (2005)
<i>Gossypium hirsutum</i>	Chlorotic spots between the main veins of topmost leaves. Youngest leaves became equally chlorotic except a dark green area around the petiole. Shortened internodes, red spots developed on the leaf blade and on parts of the veins.	Ghoneim and Bussler (1980)
<i>Carica papaya</i>	Depression in growth, appearance of chromatic spots in the interveinal areas. Flowers do not form in severe condition.	Samant (2009)
<i>Brassica nigra</i>	Younger leaves show deep purple colour which moves towards midrib. Small circular spots of purple colour are also seen and with advancement of time these spots become bleached. The plant becomes stunted and flowering/maturing is delayed.	Samant (2009)
<i>Arachis hypogaea</i>	Reduced leaf size with light yellow colour. Rosette appearance of internodes. Plants become stunted and kernel becomes shrivelled.	Samant (2009)
<i>Oryza sativa</i>	Leaves develop brown blotches and streaks that may fuse to cover older leaves entirely, stunted growth and in severe cases may die, delay in maturity and reduction in yield.	Neue and Lantin (1994)
<i>Avena sativa</i>	The leaves become pale green.	Alloway (2004)
<i>Zea mays</i>	Yellow striping of leaves, formation of white bud, stunted due to shortened internodes and the lower leaves show a reddish or yellowish streak.	Alloway (2004)

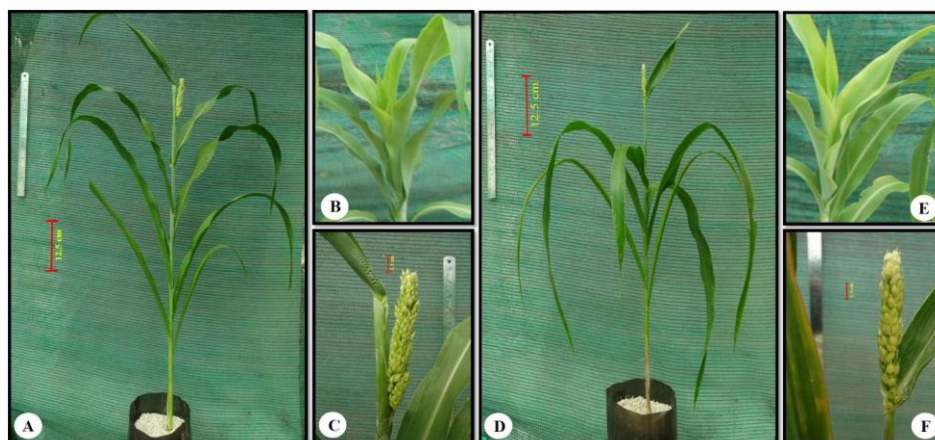


Figure 1. Zn deficiency symptoms in sorghum (APK-1). The sorghum plant grown under Zn deficient (0.00 μ M) and Zn sufficient (1.00 μ M) condition. A, B and C show characteristic features of sorghum grown under Zn sufficient condition. D, E and F show characteristic features of sorghum grown under Zn deficient condition. Under Zn deficient condition sorghum shows stunted growth especially reduction in plant height, number of leaf, length and width (D), youngest leaves with light yellow colour (E), small-sized flowers with poor grain filling, retarded development and maturation of seed (F) compared to Zn sufficient condition (A, B and C).

Biochemical studies

Zn is an essential structural component of enzymes like Cu/Zn superoxide dismutase (SOD) and carbonic anhydrase (CA) (Singh *et al.*, 2005). The activities of these enzymes may be used as indicators of Zn deficiency in plants. Generally, lower levels of Zn decreased the activities of these enzymes in many species (Kabir *et al.*, 2014). A Zn-efficient wheat genotype showed decreased activity of CA compared to a Zn-inefficient genotype in Zn deficiency condition (Rengel, 1995). The expression and activities of the Zn requiring enzymes Cu/Zn SOD and CA were also associated with Zn-efficient genotypes of wheat (Hacisalihoglu *et al.*, 2003). Expression levels of Cu/Zn SOD were elevated in Zn-efficient genotypes of wheat (Hacisalihoglu *et al.*, 2003). The activities of these enzymes were also decreased in *Vinga mungo* (black gram) during Zn deficiency (Pandey *et al.*, 2002). Similar responses were obtained in enzyme studies in bread wheat, durum wheat and rye in Zn deficiency (Cakmak *et al.*, 1997a). Further molecular studies confirmed that expression of Cu/Zn SOD genes was induced in Zn-efficient wheat genotypes compared to Zn-inefficient genotypes in Zn deficiency (Hacisalihoglu and Kochian, 2003).

Plant root exudates can help overcome Zn deficiency by increasing the bioavailability of Zn to plants. The genotypic difference in Zn acquisition from the soil may be linked to composition of root exudates released by each genotype (Marschener, 1998). The low molecular weight organic acids such as citrate, malate, nitric oxide, oxalic acid, acetic acid and amber acid are involved in the mobilization of Zn under Zn deficiency (Li *et al.*, 2012). Similarly, citrate efflux also helps uptake higher amount of Zn in low Zn, and the process is genotype dependent in rice (Hoffland *et al.*, 2006). Studies in rice confirmed that release of low molecular weight organic acid anion like malate was increased by up to 64% in low Zn supply compared to adequate Zn supply (Gao *et al.*, 2009). These studies provided evidence that root exudates helped improve Zn uptake during Zn deficiency. Identification of genotypes with efficient release of organic acid anion may help

uptake Zn more efficiently in low Zn conditions. Similarly, phytosiderophores helped uptake Zn more efficiently in low Zn conditions in barley (Erenoglu *et al.*, 2000). Crop plants like sorghum and wheat significantly increased phytosiderophore efflux in response to Zn deficiency (Hopkins *et al.*, 1998).

Mechanism of Zn uptake and translocation in plants

Zn is absorbed from soil as Zn²⁺ and transported through xylem to shoot (Clemens, 2001; Hart *et al.*, 1998). Zn is transported from soil through the root plasma membrane. The rate of Zn uptake depends on uptake efficiency of the root system, Zn concentration at the root surface and permeability of the cell membrane (Shukla *et al.*, 2014). Zn enters the plant from the soil through membrane bound transporters (Hacisalihoglu and Kochian, 2003). These transporters are involved in absorption of Zn from the soil, transport within the plant, xylem loading and unloading, vacuolar sequestration and remobilization from the vacuole. Many types of Zn transporters have been identified and their function has been characterized in plants (Figure 2; Table 2). These include Zn-regulated, iron-regulated transporter-like protein (ZIP), plasma membrane type ATPase (P-type ATPase), cation diffusion facilitator (CDF), plant cadmium resistance (PCR) and cation exchanger (CAX). Apart from Zn, most of these transporters are also involved in the transport of other cations viz. manganese (Mn), iron (Fe), cadmium (Cd), cobalt (Co) and copper (Cu). The details of some of these transporters are discussed below.

ZIP

The ZIP family comprises more than a hundred transporters found at every phylogenetic level (Grotz and Guerinot, 2006). The ZIP transporters have eight transmembrane (TM) domains, with their amino and carboxyl ends exposed to the external surface of the plasma membrane (Guerinot, 2000). Besides Zn, ZIP also transports various other metal ions (Mn, Fe, Cd, Co, Cu and Ni) (Pedas and Husted, 2009). The functions of ZIP transporters have been

Table 2. Details of various Zn transporters reported in plants.

Plant name	Transporter family	Transporter name	Metal transport function	References
<i>Medicago truncatula</i>	ZIP	<i>MtZIP1, MtZIP5, and MtZIP6</i>	Zn	Lopez-Millan <i>et al.</i> (2004)
<i>Manihot esculenta</i>	ZIP	<i>MeZIP</i>	Zn	Bamrungsetthapong <i>et al.</i> (2010)
<i>Triticum aestivum</i>	ZIP	<i>TaZIP1</i>	Zn	Durmaz <i>et al.</i> (2011)
<i>Hordeum vulgare</i>	ZIP	<i>HvZIP7</i>	Zn, Fe, Mn and Cu.	Tiong <i>et al.</i> (2009)
	CDF	<i>HvMTP1</i>	Zn and Co	Podar <i>et al.</i> (2012)
	ZIP	<i>HvIRT1, HvZIP5</i>	Zn	Pedas and Husted (2009)
	P-type ATPase	<i>HvHMA2</i>	Zn and Cd	Mills <i>et al.</i> (2012)
<i>Zea mays</i>	ZIP	<i>HvZIP7</i>	Zn	Tiong <i>et al.</i> (2014)
	ZIP	<i>ZmZIP1, ZmZIP2, ZmZIP3, ZmZIP4, ZmZIP5, ZmZIP6, ZmZIP7, ZmZIP8 and ZmIRT1</i>	Zn and Fe	Li <i>et al.</i> (2013)
<i>Arabidopsis</i>	ZIP	<i>AtZIP1, AtZIP2, AtZIP3, AtZIP4, AtZIP5, AtZIP6, AtZIP7, AtZIP8, AtZIP9, AtZIP10, AtZIP11 and AtZIP12</i>	Zn	Jain <i>et al.</i> (2013)
	ZIP	<i>AtIRT1 and AtIRT2</i>	Zn and Fe	Henriques <i>et al.</i> (2002)
	CDF	<i>AtMTP1</i>	Zn	Tanaka <i>et al.</i> (2013); Kobe <i>et al.</i> (2004)
	CAX	<i>AtMHX1</i>	Zn	Shaul <i>et al.</i> (1999)
	ZIP	<i>AtZIP1, AtZIP2, AtZIP3 and AtZIP4</i>	Zn	Grotz <i>et al.</i> (1998)
	CDF	<i>AtZAT1</i>	Zn	Bloß <i>et al.</i> (2002)
	ZIP	<i>AtIRT3</i>	Zn and Fe	Lin <i>et al.</i> (2009)
	PCR	<i>AtPCR2</i>	Zn	Song <i>et al.</i> (2010)
	P-type ATPase	<i>AtHMA2 and AtHMA4</i>	Zn	Hussain <i>et al.</i> (2004)
	<i>Oryza sativa</i>	ZIP	<i>OsZIP8</i>	Zn
P-type ATPase		<i>OsHMA3</i>	Zn	Sasaki <i>et al.</i> (2014)
ZIP		<i>OsZIP4</i>	Zn	Ishimaru <i>et al.</i> (2005)
ZIP		<i>OsZIP1 and OsZIP3</i>	Zn	Ramesh <i>et al.</i> (2003)
ZIP		<i>OsZIP1, OsZIP3 and OsZIP4.</i>	Zn	Chen <i>et al.</i> (2008)
ZIP		<i>OsZIP8</i>	Zn	Lee <i>et al.</i> (2010)
<i>Populus spp.</i>	CDF	<i>PtdMTP1</i>	Zn	Blaudez <i>et al.</i> (2003)
<i>Vitis vinifera</i>	ZIP	<i>VvZIP3</i>	Zn	Gainza-Cortés <i>et al.</i> , (2012)
<i>Glycine max</i>	ZIP	<i>GmZIP1</i>	Zn	Moreau <i>et al.</i> (2002)

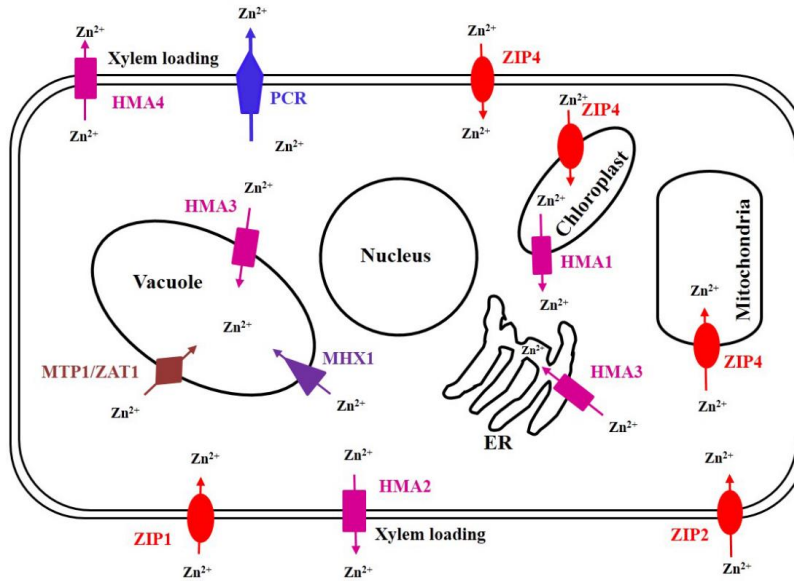


Figure 2. Localization of various Zn transporters in plant cell. Zn transporter family is actively involved in uptake, transport, detoxification and homeostasis of Zn within plants. Depending on the Zn concentration in soil, various types of Zn transporters are expressed. During deficient concentration of Zn, ZIP (ZIP1, ZIP2 and ZIP4) and P-Type ATPase (HMA2) families of Zn transporters are induced which transport Zn into the cell through plasma membrane from the soil, and then CAX (MHX1), CDF (MTP1 and ZAT1), P-Type ATPase (HMA2 and HMA4) and ZIP (ZIP4) families of transporters are involved in mobilization of Zn into organelles. The PCR family member PCR2 is important for redistribution and detoxification Zn. The P-Type ATPase family member HMA1 is involved in detoxification of Zn in chloroplast. Studies on localization and transport activity of ZIP transporters are still under progress.

investigated in several species, such as *Medicago truncatula* (barrel medic) (Lopez-Millan *et al.*, 2004), barley (Tiong *et al.*, 2009; Pedas and Husted, 2009; Tiong *et al.*, 2014), maize (Li *et al.*, 2013), rice (Lee *et al.*, 2010; Chen *et al.*, 2008; Ishimaru *et al.*, 2005; Ramesh *et al.*, 2003; Yang *et al.*, 2009), *Arabidopsis* (Grotz *et al.*, 1998; Henriques *et al.*, 2002; Lin *et al.*, 2009), *Manihot esculenta* (cassava) (Bamrungsetthapong *et al.*, 2010) wheat, (Durmaz *et al.*, 2011), *Vitis vinifera* (grape) (Gainza-Cortés *et al.*, 2012) and *Glycine max* (soybean) (Moreau *et al.*, 2002). The ZIP transporters are highly expressed in roots in Zn deficiency. In *Arabidopsis*, 15 ZIP family members were identified (Mäser *et al.*, 2001) and most of these were induced in response to Zn deficiency. Functions of AtZIP1, AtZIP2, AtZIP3 and AtZIP4 were tested in the Zn uptake deficient yeast mutant (*zrt1 zrt2*) and all these

four genes were able to complement yeast mutant (Grotz *et al.*, 1998). ZIP1 and ZIP3 genes are induced in roots and ZIP4 is induced in root and shoots in Zn deficiency (Grotz *et al.*, 1998; Wintz *et al.*, 2003). ZIP9 is also induced in Zn deficiency in *Arabidopsis* (Talke *et al.*, 2006). Another ZIP family transporter, iron-regulated transporter 3 (*IRT3*), was also identified in *Arabidopsis halleri* and *A. thaliana* and its function was characterized (Lin *et al.*, 2009). *IRT3* from both species of *Arabidopsis* was able to complement *zrt1, zrt2* and Fe-uptake deficient mutant (*fet3, fet4*) confirming the transport ability of Zn and Fe. Localization studies confirmed the expression of *IRT3* in plasma membrane (Lin *et al.*, 2009).

CDF

The CDF is a large and ubiquitous metal transporter family. It is another Zn transporter found in both prokaryotes and eukaryotes (Guffanti *et al.*, 2002). CDF family of transporters plays a vital role in heavy metal homeostasis in plants (Blaudez *et al.*, 2003). It is a proton antiporter, and transports metals such as Zn, Fe, Co, Ni, Cd, and Mn (Gustin *et al.*, 2011). Many members of CDF family have been implicated in the transport of Zn in plants (Gaither and Eide, 2001). The CDF family proteins have six putative TM domains (Eide, 2006). Metal tolerance proteins (MTPs) are another group of metal transporters belonging to the CDF family and are highly specific to Zn (Krämer, 2005). Some members of CDF family are found on both plasma membrane and vacuole membrane and are involved in the uptake and redistribution of heavy metals. The identification of CDF family members like Zinc *Arabidopsis* transporter (ZAT)/MTP1 on the vacuolar membrane revealed a possible vacuolar transporter of Zn in plants (Yang and Chu, 2011). The CDF family members have been identified and characterized in plants such as barley (Podar *et al.*, 2012) and *Arabidopsis* (Bloß *et al.*, 2002; Kobae *et al.*, 2004; Tanaka *et al.*, 2013), and *Populus spp.* (Blaudez *et al.*, 2003).

CAX

Members of CAX family have been identified in animals, plants, fungi, and bacteria (Shigaki *et al.*, 2006). The CAX transporters are divalent cation/H⁺ antiporters and are located on the vacuoles, which are involved in cation transport in plants (Jain *et al.*, 2009). It contains 10-14 TM domains (Hanikenne *et al.*, 2005). The CAX family members were primarily found to transport Ca²⁺; further studies revealed their ability to transport a wide range of ions including Zn (Socha and Guerinot, 2014). Mg²⁺/H⁺ exchanger (MHX) is also a member of CAX family, which is an H⁺ antiporter, localized in the vacuolar membrane and involved in transport of Mg and Zn across the tonoplast in *Arabidopsis* (Shaul *et al.*, 1999). CAX family of transporters is crucial for the redistribution of cations

including Zn in *Arabidopsis* (Socha and Guerinot, 2014). These transporters were identified and characterized in *Arabidopsis* (Shigaki *et al.*, 2006; Shaul *et al.*, 1999) and rice (Kamiya *et al.*, 2005).

P-type ATPase

The P-type ATPase family of transporters was identified in both prokaryotes and eukaryotes (Hussain *et al.*, 2004; Rastgoo *et al.*, 2011; Wang *et al.*, 2014). Heavy metals including Zn are transported across the membrane against their electrochemical gradient by the energy of ATP hydrolysis (Møller *et al.*, 1996). The structures of P-type ATPases contain eight TMs and a CPx/SPC signature motif is found in sixth TM, which has a key role in metal binding and translocation (Williams and Mills, 2005). The function of P-type ATPases has been proved in transition metal transport and homeostasis in *Arabidopsis* (Williams and Mills, 2005). Heavy metal ATPase (HMAs) is one of the members of the P-type ATPase (Hussain *et al.*, 2004) which is involved in transport of Cu, Zn, Cd, lead (Pb), and Co (Rensing *et al.*, 1999). Hussain *et al.* (2004) reported that HMA2 and HMA4 were involved in Zn transport and played an essential role for increasing the Zn content in roots, stems, and leaves of *Arabidopsis*. Xylem-loading is an important step for the translocation of Zn from root to rest of the plant. The HMA2 and HMA4 family of transporters is involved in xylem loading of Zn in xylem parenchymatous cells (Hussain *et al.*, 2004; Hanikenne *et al.*, 2008; Sinclair and Krämer, 2012). The role of *AtHMA1* gene was tested in 3 different *hmal* knock out *Arabidopsis* mutants (*hmal-1*, *hmal-2* and *hmal-3*) in Zn toxicity (Kim *et al.*, 2009). This study confirmed Zn detoxification function of *AtHMA1* and it has been found to be localized on chloroplast envelope. The Zn transporting activity of *AtHMA1* was also tested in Zn sensitive *zrc1* yeast mutant and it confirmed that expression of *AtHMA1* exacerbated the sensitivity of *zrc1* in the excess Zn (Kim *et al.*, 2009). Many P-type ATPase family members have been identified and characterized in plants viz. *Arabidopsis* (Hussain *et al.*, 2004), rice (Sasaki *et al.*, 2014) and barley (Mills *et al.*, 2012).

PCR

PCR transporter is the largest gene family and the members of these metal transporters are found in fungi, algae, plants and animals (Song *et al.*, 2011). These transporters act as secondary transporters mainly in epidermal cells and in the xylem of new roots. In *Arabidopsis*, PCR2 gene was found to be expressed both in roots and shoots and is involved in plant survival in excess and deficient conditions of Zn. PCR2 is also important for redistribution and detoxification of Zn in plants like *Arabidopsis* (Song *et al.*, 2010). The main role of PCR2 is the transporting of Zn and maintaining of optimal Zn concentration in roots of *Arabidopsis*.

Agronomic aspects of managing low Zn in soil

Many agronomic aspects are to be taken into consideration while managing the soils with low Zn that affect both the growth and yield of crop plants. The effects of warmer temperatures, dry soils, soil microbial activity and root-induced chemicals help largely in the Zn uptake from the soil by plants. Improvements of agronomic factors may influence chemical and physical processes in soils that influence the nutrient availability (Pilbeam, 2015). When soil temperature is low, mineralization of soil organic matter slows down resulting in less amount of Zn release in the soil. The application of green leaf manuring is one of the important practices for increasing organic matter and Zn content in the soil. For example, the application of 1 t/ha of *Gliricidia* (*Gliricidia sepium*) leaf manure provides 85g Zn in soil (Srinivasara and Rani 2011). Also, the incorporation of whole parts of horse gram (*Macrotyloma uniflorum*) into soils showed increase in the availability of Zn in soil (Venkateswarlu *et al.*, 2007). Manzeke *et al.* (2012) reported that the supply of quality organic nutrient resources apparently had a strong influence on available Zn in soil. Remarkably, the application of farmyard manure showed relatively higher status of existing Zn content in soil (Srinivasarao *et al.*, 2013).

Mixed cropping and intercropping systems are common and most important for the nutritional improvement of crops grown in nutrient-poor soils or low-input agro-ecosystems

(Li *et al.*, 2004; Zuo and Zhang, 2008). These agro-systems may have numerous advantages in terms of increasing availability of Zn (Zuo and Zhang, 2008). The crucial role played by the interspecific root contacts in nutrient acquisition in mixed stands of plants was also reported (Li *et al.*, 2001). Manzeke *et al.* (2012) suggested that the legume-cereal intercropping system proved a possible avenue for improving plant available soil Zn. This is due to the high capacity of legumes to scavenge nutrients from the soil and release it back to the soil through falling off (Zuo and Zhang, 2008). In field study, intercropping system had higher Zn concentration in shoot and seed of wheat and chickpea compared to monocropping system (Li *et al.*, 2001).

In farming, the greatest management practices and the best external alternative are to supply Zn to low Zn soil. The application of inorganic Zn containing fertilizers maintains or restores Zn content in soil (Rengel 2002). With wide range of soil types, the addition of Zn fertilizer varies and it ranges from 0.5 to 1.5 kg/ha (Takkar *et al.*, 1989). Zn containing fertilizers like Zn sulphate heptahydrate (21%), Zn sulphate monohydrate (33%), Zn-EDTA (12%), zincated urea (2%) and zincated phosphate (17.6%) are widely used to address Zn deficiency problem all over the world (Cakmak *et al.*, 2010; Das *et al.*, 2013). Zn fertilizers provide an immediate and effective remedy to increase Zn concentration under soil with severe Zn stress. Similarly, the foliar application of Zn is also a quick solution to plants growing in low Zn soil. Supplying Zn through seed soaking and seed coating are also other agro-practices that result in increased crop yields in low Zn soils (Rengel, 2002). When compared, the seed treatment gave higher ZUE than soil application of Zn sulphate at the rate of 5.5 kg Zn ha⁻¹ (Singh *et al.*, 2003).

Crop varieties respond differently to varying systems of fertility management and the mechanisms for the uptake of different nutrients from soil also differ (Valizadeh *et al.*, 2002). ZUE genotypes contribute not only to reduce the costs of fertilizer inputs but also to overcome the problems related to subsoil Zn deficiency (Torun *et al.*, 2000). A genotype with high nutritional-use efficiency gives high yields in infertile soil.

In many crop plants genetic variation with respect to ZUE has been validated (Graham and Rengel 1993; Erenoglu *et al.*, 2000; Fageria 2001; Lonergan *et al.*, 2009; Yamunarani *et al.*, 2016). The Zn deficiency tolerant genotypes are designed to manage low Zn in soil.

Efforts made to improve ZUE

Efforts have been made by researchers to improve ZUE of plants using various approaches including, conventional breeding, transgenic modification and marker assisted breeding. The details of conventional breeding, transgenic and marker assisted breeding (MAB) approaches made to improve the ZUE are presented below.

Conventional breeding approach

Conventional breeding has been used to improve agricultural production for thousands of years in several biotic and abiotic stress conditions. Hybridization is the most common method of creating genetic variation with improved characteristics. Plant breeding strategies hold great promise for making a significant low-cost and sustainable contribution to improve Zn uptake. The ZUE may be improved through conventional plant breeding by selecting genotypes on the basis of genetic variability. These genotypes are used to develop ZUE lines. Germplasm screening can be used to raise ZUE in plants. Many Zn deficiency tolerant crop plants in Zn deficient condition were characterized and reported (Rengel and Römheld, 2000; McDonald *et al.*, 2008).

ZUE plants have been successfully developed in few crops. For example, the dry land rice cultivar was developed from crossing IR74 (intolerant) and Jalmagna (tolerant) (Wissuwa *et al.*, 2006). This dry land rice cultivar exhibited significant genotypic variation in tolerance to low soil Zn (Gao *et al.*, 2006). Similarly, the sorghum hybrid variety CSH-7 (36-A × 168) showed greater capacity to absorb Zn in soil (Ramani and Kannan 1985). The doubled haploid barley population was developed from crossing two genotypes, Clipper (low Zn accumulator) and Sahara 3771 (high Zn accumulator). While screening this population, some of the lines showed higher Zn uptake

efficiency than parental lines (Lonergan *et al.*, 2009). The hexaploid wheat line derived from the crossing between Miracle wheat (*Triticum turgidum*) and Einkorn wheat (*Triticum monococcum*) had a significant increase in the total amount of Zn in shoot with increased shoot and root growth under Zn deficient conditions (Cakmak *et al.*, 1999). Similarly, the synthetic hexaploid wheat lines (*Triticum durum* × *Aegilops tauschii*) had higher Zn content in its grains than other cultivated wheats (Calderini and Ortiz-Monasterio 2003). The ZUE contributed to higher Zn uptake efficiency which was responsible for the higher grain Zn concentration in the hexaploid wheat lines. Many more efforts are needed to develop ZUE plants through conventional breeding. It will ensure to improve growth and yield of important crop plants in low Zn soil without relying much on synthetic Zn fertilizers.

Transgenic approach

Plant genetic engineering has been considered as a straight forward approach for imparting specific trait in crop plants. Genes of many Zn transporters have been overexpressed in various plants through transgenic modification to improve the ZUE. Overexpression of these transporters increased the Zn uptake in Zn deficiency. For example, overexpression of *AtZIP1* increased plant growth and Zn transport rates in *Arabidopsis* in Zn deficiency condition (Ramesh *et al.*, 2004). Similarly, overexpression of *Arabidopsis AtMTP1* and *AtZIP1* genes in cassava improved the accumulation of Zn in the edible portion of the storage root compared to control plants in Zn deficiency (Gaitán *et al.*, 2015). Also, several other Zn transporters (*OsZIP4*, *AtZIP1*, *AtMHX1*, *AtMPT1*, *AhHMA4*, *ZmIRT1*, *ZmZIP3* and *NcTZN1*) were overexpressed in rice, *Arabidopsis* and *Nicotiana tabacum* (tobacco) to improve Zn acquisition during Zn deficiency (Table 3).

Molecular marker approach

Molecular marker assisted selection (MAS) and breeding are also utilized for the improvement of crop plants for many agronomically important traits such as grain yield, quality, disease

resistance, nutritional quality, etc (Genc *et al.*, 2009; Hash *et al.*, 2002; Srinives *et al.*, 2010). The identification of quantitative trait loci (QTL) provides the basis for devising plant breeding strategies to improve ZUE through marker assisted selection. These approaches can be used to develop new genotypes with improved ZUE

in various crop plants. However, only little effort has been made so far in utilizing molecular markers to improve ZUE in crop plants. Nagesh *et al.* (2013) reported that QTL SC129 was associated with ZUE in rice. This QTL is located on chromosome number 3. In barley, microsatellite-anchored fragment length

Table 3. The details of Zn transporter genes overexpressed in various plants through transgenic modification.

Transformed species	Name of the gene	Source of the gene	Function	References
<i>Oryza sativa</i>	<i>OsZIP4</i>	<i>Oryza sativa</i>	Zn transport and distribution	Ishimaru <i>et al.</i> (2007)
<i>Hordeum vulgare</i>	<i>AtZIP1</i>	<i>Arabidopsis</i>	Zn uptake	Ramesh <i>et al.</i> (2004)
<i>Manihot esculenta</i>	<i>AtMTP1</i> and <i>AtZIP1</i>	<i>Arabidopsis</i>	Zn accumulation	Gaitán-Solís <i>et al.</i> (2015)
<i>Arabidopsis</i>	<i>ZmIRT1</i> and <i>ZmZIP3</i>	<i>Zea mays</i>	Zn accumulation	Li <i>et al.</i> (2015)
<i>Nicotiana tabacum</i>	<i>AtMHX1</i>	<i>Arabidopsis</i>	Zn transport	Shaul <i>et al.</i> (1999)
<i>Nicotiana tabacum</i>	<i>NcTZNI</i>	<i>Neurospora crassa</i>	Zn accumulation	Dixit <i>et al.</i> (2010)
<i>Nicotiana tabacum</i>	<i>AhHMA4</i>	<i>Arabidopsis</i>	Zn accumulation	Barabasz <i>et al.</i> (2010)

polymorphism (MFLP) marker SZnR1 has been found to be associated with Zn concentration and content (Sadeghzadeh *et al.*, 2010). Similarly, Nawaz *et al.* (2015) reported that QTL RM237, RM3562, RM6863 and RM105 were associated with grain Zn concentration of brown rice. These markers are located on chromosome numbers 1, 3, 8, and 9 respectively. Several other reports are also available for the identification of QTL for Zn content of rice grains. Four candidate genes (*OsNAC*, *OsZIP8a*, *OsZIP8c* and *OsZIP4b*) were also found to be connected with the Zn content of rice grain (Gande *et al.*, 2015). Similarly, markers for candidate genes *OsARD2*, *OsIRT1*, *OsNAS1* and *OsNAS2* were found to be associated with the grain Zn content of rice (Anuradha *et al.*, 2012). QTL were also identified for leaf bronzing (*Zbz1a*, *Zbz1b*, *Zbz4*, *Zbz7* and *Zbz12*), plant mortality (*Zmt1*, *Zmt2*, *Zmt7* and *Zmt12*) and dry matter (*Zdm7*, *Zdm3*, *Zmt2*, and *Zmt12*) in Zn deficient conditions in rice (Wissuwa *et al.*, 2006). Most of these marker studies so far focused on rice only; only a few studies have been performed on other plants to find the marker for ZUE. Gelin *et al.* (2007) found QTL associated with Zn content of the seed in

recombinant inbred lines (RILs) of *Phaseolus vulgaris* (navy bean). Roshanzamir *et al.* (2013) identified the QTL associated with Zn concentration of bread wheat grain using composite interval mapping (CIM). Similarly, QTL are also identified using CIM for Zn concentration/content in wheat, rice, *Arabidopsis*, barley etc. (Table 4). These QTL could be used for marker assisted selection and breeding for developing new genotypes with improved ZUE in the same or other plants. The candidate genes and molecular markers established through basic research in model plants like *Arabidopsis* could be extended to other crops to improve their ZUE.

CONCLUSION

In conclusion, Zn deficiency is a major problem for crop production worldwide. It has caused yield losses in major crops such as rice, maize and wheat. Currently, the non-conventional or advanced molecular plant breeding techniques help improve ZUE in crop plants. MAB and transgenic are two widely used plant breeding techniques to produce plants with favorable

Table 4. Details of quantitative trait loci (QTL) for grain Zn content detected by composite interval mapping (CIM) in various plants.

Name of the plant	Traits identified	Chromosome position	Detail of markers	Reference
<i>Triticum aestivum</i>	Grain Zn content and concentration	1A	P3156.2-WMC59	Shi <i>et al.</i> (2008)
		2D	P3470.3-P3176.1	
		3A	Xgwm391-P8422	
	Grain Zn content	4A	P3446-205-CWM145	
		4D	WMC331-Xgwm624	
		5A	WMC74-Xgwm291	
		7A	WMC488-P2071-180	
<i>Triticum aestivum</i>	Grain Zn concentration	1A	Xgwm3094-Xgwm164	Roshanzamir <i>et al.</i> (2013)
		4A	Xgwm4026-Xgwm1081	
<i>Oryza sativa</i>	Grain Zn concentration	1	RM34-RM237	Stangoulis <i>et al.</i> (2007)
		12	RM235-RM17	
<i>Oryza sativa</i>	Grain Zn concentration	4	CT206-G177	Zhang <i>et al.</i> (2011)
		6	RZ516-G30	
<i>Arabidopsis</i>	Grain Zn content	1	AXR1	Vreugdenhil <i>et al.</i> (2004)
		2	FD150	
		3	FD111	
		5	HH480	
<i>Hordeum vulgare</i>	Grain Zn concentration	2HS	bcd175 - psr108	Sadeghzadeh <i>et al.</i> (2015)
		2HL	vrs1 - ksuF15	
		3HL	wg178 - HVM60	
		4HS	cdo358 - awbma29	
	Grain Zn content	2HS	bcd175 - psr108	
		2HL	vrs1 - ksuF15	
<i>Zea mays</i>	Grain Zn concentration	4-08	ZM136	Simic <i>et al.</i> (2012)
		3-05	bnlg1456	
<i>Triticum aestivum</i>	Shoot Zn content	3A	Xmwg30	Balint <i>et al.</i> (2007)
		7A	Xcdo545b	
<i>Oryza sativa</i>	Grain Zn content	2	RM521-RM29	Kumar <i>et al.</i> (2014)
		10	RM473-RM184	
		10	RM496-RM591	
<i>Triticum aestivum</i>	Grain Zn content	7A	Xcfd31 – Xcfa2079	Singh <i>et al.</i> (2008)
<i>Triticum aestivum</i>	Grain Zn concentration	2D	wPt-730057-wPt-671700	Pu <i>et al.</i> (2014)
		3D	wPt-6191-wPt-8658	
		4D	wPt-671648-wPt-667352	
		5B	wPt-7237-wPt-0708	
<i>Triticum aestivum</i>	Grain Zn concentration	3D	Gdm136-gwm3	Genc <i>et al.</i> (2009)
		4B	Wms149-gmw113	
		6B	Barc146a-p41/M48-76	
		7B	Gwm282-gwm63	

traits such as Zn-use efficiency. The plants produced by MAB have already been accepted worldwide unlike the transgenic plants that face the challenge with regard to safety on human health. Zn transporters play an important role to maintain Zn uptake during Zn deficiency condition. Only a little information is available on the mechanism of Zn homeostasis in crop plants. Many types of Zn transporters are involved in uptake and translocation of Zn in plants. Further characterization of these transporters is crucial to understand the mechanism behind the acquisition and transport of Zn in crop plants. QTLs have been identified using molecular markers. Most of the molecular marker studies are focused on rice only. The QTL needs to be identified for ZUE in other major cereals such as maize, wheat and millets.

Conventional and non-conventional plant breeding techniques play an important role in crop improvement. A collective effort coupled with research is needed especially in the developing world to improve the crop plants for ZUE using MAB.

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