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Role of ZIP Family Transporters in Zinc Uptake and Transport in Plants: Implications for Biofortification and Zinc Deficiency Mitigation

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Authors' contributions

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

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ABSTRACT

Zinc (Zn) is an essential micronutrient crucial for the physiological and biochemical processes in plants. Approximately 50% of global agricultural soils are Zn-deficient, leading to reduced crop yield and quality. The intricate balance of Zn uptake and homeostasis is most important for optimal plant growth and development, and its efficient uptake and transport within plants are facilitated by various families of metal transporters, including zinc-regulated transporter (ZRT)/iron-regulated

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transporter (IRT)-like protein (ZIP) family transporters through cellular uptake, intracellular trafficking, and detoxification of Zn in plants. ZIP transporters also exhibit the ability to transport other divalent metal cations, including Cd^{2+}, Fe^{2+}, and Cu^{2+}. homeostasis. This paper reviews the role of ZIP transporters in Zn transport, focusing on their identification, characterization, and expression patterns in different plant species such as rice, maize, wheat, barley, and foxtail millet. Furthermore, it discusses the potential of manipulating ZIP transporter genes for biofortification purposes to enhance Zn content in crops, thereby addressing global zinc deficiency issues.

Keywords: Zinc; Zinc-Regulated Transporter (ZRT); Iron-Regulated Transporter (IRT).

1. INTRODUCTION

Zinc (Zn) is one of the most important irreplaceable micronutrients essential for normal agriculture production. Zinc deficiency poses a significant challenge to global agriculture and human nutrition. Regmi *et al*., (2010) highlighted the significant nutritional challenge posed by zinc deficiency in humans, affecting over 3 billion individuals globally. This deficiency leads to various health issues due to insufficient zinc intake through food. For instance, around half of paddy fields suffer from zinc deficiency, resulting in low yields and poor nutritional quality of rice grown in these areas (Krithika & Balachandar, 2016). To overcome low Zn availability, plants acquire zinc from the soil primarily as divalent ions (Zn^{2+}), facilitated by specialized metal transporters known as ZIP family transporters. These transporters play crucial roles in Zn uptake, distribution, and homeostasis within plants. Besides Zn transport, ZIP proteins transport divalent ions such as Fe^{2+}, Zn^{2+}, Mn^{2+}, and Cd^{2+} (Kumar et al., 2016). Understanding the expression patterns, localization, and functions of ZIP transporters across various plant species is essential for developing strategies to enhance Zn uptake and accumulation in crops, particularly under conditions of Zn deficiency. This paper provides a comprehensive overview of the current knowledge regarding ZIP transporters in different crops, highlighting their importance in Zn transport and their potential for biofortification to address zinc deficiency issues.

2. ZINC UPTAKE IN PLANTS

Plants have developed various methods to absorb, transport and store Zn because of the varying requirements of each plant. Zn homeostasis very essential in plants since a slight increase or decrease in concentration will lead to toxicity or deficiencies. Therefore, plants have adopted different strategies to maintain Zn homeostasis. Fig. 1 depicts the Zn uptake of plants. Most of the Zn uptake by plant roots is in the form of Zn^{2+}, but in certain cases organic ligand-Zn complexes are also absorbed by plants. There are two main strategies for Zn uptake in plants. First, Zn complexes are dissolved as Zn^{2+} for easy absorption by the release of reductants, organic acids and H^+ ions. Second method involves formation of stable Zn complexes by the release of phytosiderophores which is then absorbed by roots. But this method is restricted to cereals. Phytosiderophores are non-protein amino acids which has high binding affinity. Passive absorption of Zn^{2+} by roots is done through mass flow and diffusion. This cation uptake mechanism is driven by RCPM H^+-ATPase system (Gupta et al., 2016). After entering, roots these divalent ions (Zn^{2+}) move towards vascular systems where it take two pathways- apoplastic and symplastic. Symplastic pathway involves the movement of Zn^{2+} ions through plasmodesmata between the cells forming a continuous pathway from plasma membranes to root cells. Apoplastic pathway involves extracellular movement of Zn^{2+} ions towards endodermis where casparian strip act as a barrier so that Zn^{2+} ion movement takes place through plasma membrane into endodermal cells The movement of Zn^{2+} ion across plasma membrane toward xylem requires metal transporters for their transport (Stanton et al., 2022). P1B-ATPase, zinc-regulated transporter (ZRT), iron-regulated transporter (IRT)-like protein (ZIP), natural resistance-associated macrophage protein (NRAMP), and cation diffusion facilitator (CDF) are just a few of the metal transporter families that have been extensively identified and shown to be involved in metal uptake and transport in plants, archaea, bacteria, fungi, and mammals in recent years (Kumar et al., 2016).

3. ROLE OF ZINC TRANSPORTERS IN ZN TRANSPORT

Zinc is acquired and transported as divalent ion (Zn^{2+}) in plants. Zinc transporters are required to transport Zn into the cytoplasm because Zn cannot diffuse into the cell membrane.ZIP family transporters are mainly known to contribute in the uptake, distribution, and transit of zinc throughout the entire plant. Therefore, it plays a major role in Zn transport and homeostasis (Krishna et al., 2020). Apart from Zn transport, ZIP proteins are involved in transport of various divalent ions such as Fe^{2+}, Zn^{2+}, Mn^{2+}, and Cd^{2+} (Kumar et al., 2016). Therefore, it is crucial to understand their expression levels, localization, and function in crops. In the future, crops that are tolerant of zinc deficiencies may be developed using biotechnological techniques. It aids in enhancing crop quality and yield, particularly in raising the zinc content of grains, and it helps address the global zinc shortage issue. Zn fortification in crops can be enhanced through genetic alteration of the ZIP transporter families (Krishna et al., 2020).

4. ZIP FAMILY TRANSPORTERS IDENTIFIED IN VARIOUS CROPS

According to Grotz *et al.*, (1998) Zn transporters were involved in transporting zinc from soil into the root. ZIP 1, ZIP 3 and ZIP 4 are zinc responsive and are their genes are expressed under zinc deficient conditions. ZIP 1 and ZIP 3 genes are induced in roots whereas ZIP 4 gene is induced in both shoots and roots. It was noted that uptake of zinc from rhizosphere was done by ZIP 1 and ZIP 3 while ZIP 4 was responsible for the transport of zinc in plastids. Model plants such as Arabidopsis and rice have been used to identify and characterise the roles of ZIP family transporter genes. Identification and characterization of the ZIP family genes are still limited to certain crops and are lacking for many crops.

The expression of 10 ZIP genes we compiled from a global gene expression map for Arabidopsis development (Schmid et al., 2005) was studied and analysed by Milner et al., (2013). From his analysis it was found that the roots express larger levels of *ZIP1, ZIP2, ZIP3, ZIP5,* and *ZIP6* than the shoots do. Additionally, as the plant ages, *ZIP1, ZIP2, ZIP3*, and *ZIP5* exhibit greater relative expression in the roots. *ZIP7* and, to a lesser extent, *ZIP11,* which displayed high shoot expression at day 7 in the shoots but subsequently saw a decline in expression as the plant aged, are the ZIP genes that showed noticeably higher expression in the shoots. When the plant grew older, *ZIP9, ZIP10*, and *ZIP12* did not exhibit any differences in expression; instead, they displayed comparatively comparable expression in both roots and shoots.

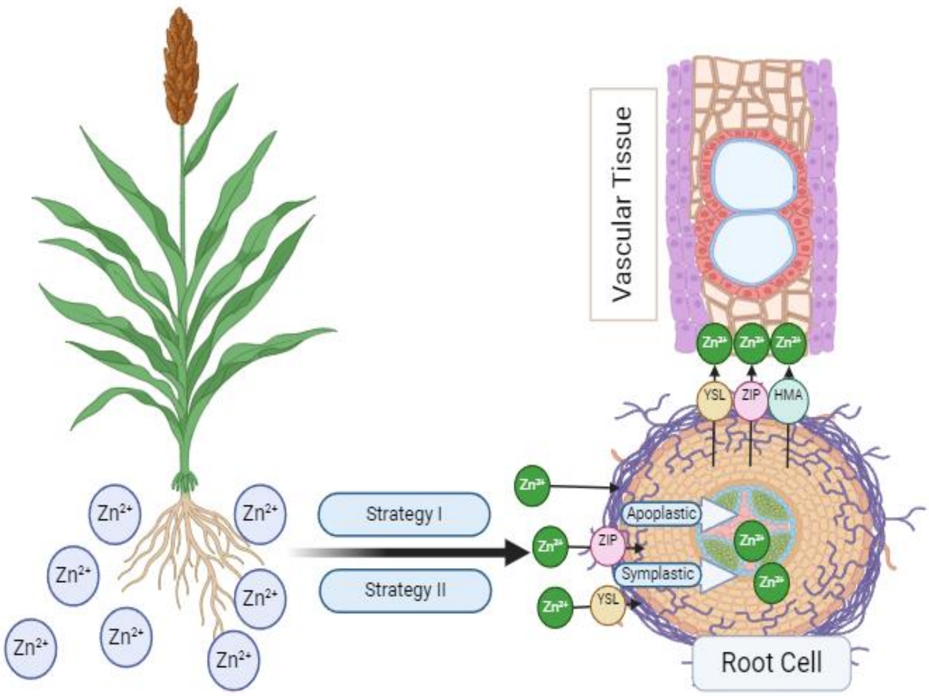

Fig. 1. Show the process of Zn^{2+} absorption and movement inside roots through different pathways and then to vascular tissues via various transporters

Table 1. The detailed characteristics of each SlZIP gene identified by different authors

Name of the plant	Name of ZIP genes	Characters	Time of Expression	Reference
Rice	OsZIP 1	Localized in vascular bundles and epidermal cells in roots which facilitates Zn uptake from soil Also expressed in epidermis and vascular tissues of roots and leaves of rice.	Under Zn starvation/ Zn deficient condition	(Bashir *et al., (2012)*; Ramesh *et al*., (2003)
	OsZIP 3	Expressed in both roots and shoots Localized in vascular bundles and epidermal cells in roots and shoots which facilitates Zn uptake from the soil.	Under both Zn sufficient and deficient conditions.	(Ramesh *et al*., (2003); Ishimaru *et al*., (2006))
		Highly expressed in nodal region which facilitates uploading of Zn from the xylem.	Under Zn Deficient conditions.	(Sasaki *et al*., (2015))
	OsZIP 4	Highly expressed in both roots and shoots Localized in vascular bundles and epidermal cells in roots and shoots	Under Zn deficient condition.	(Ishimaru *et al*., (2005))
		Also localized in plasma membrane and are involved in Zn influx.		(Ishimaru *et al*., (2005); Lee *et al*., [2010, 2010)
		Highly expressed in nodal region	Under Zn deficient condition.	(Sasaki *et al*., (2015)
		Might be responsible for Zn translocation to aerial parts.		(Ishimaru *et al*., (2011)
		Played a role in grain filling.		(Bashir *et al*., (2012)
	OsZIP 5	Localized to plasma membrane and are important for root to shoot translocation of Zn.		(Bashir *et al*., (2012); Ishimaru *et al*., (2005); Lee *et al*., (2010, 2010)
	OsZIP 7	Expressed in roots and shoots	Under Zn deficient conditions	(Yang *et al*., (2009); Tan *et al., (2019)*)
		Located in the parenchyma cells of vascular bundles in nodal region, and in the stele in the roots of rice.		(Tan *et al*., (2019)
	OsZIP 8	Played a role in grain filling		(Bashir *et al*., (2012))
		Expressed in roots and shoots	Under Zn deficient conditions	(Yang *et al*., (2009); Tan *et al.,* (2019))
		Localized to plasma membrane and involved in translocation of Zn from root to shoot		(Bashir *et al*., (2012); Ishimaru *et al*., (2005); Lee *et al*., (2009, 2010)
	OsIRT 1 & OsIRT 2	Expressed in roots and localized to plasma membrane Expression level of OsIRT 1 was much higher than OsIRT 2	Under Fe deficient condition	(Bughio *et al*., (2002); Ishimaru *et al*., (2005); Lee *et al*., (2009)
Maize	ZmZIP 1	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 2	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al.,* (2013)
		Expressed in kernel	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 3	Up-regulated in both shoot and root	Under Zn deficient condition	(Li *et al*.,(2013))
	ZmZIP 4	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 5	Induced in shoot	Under Zn deficient condition	(Li *et al*., (2013)
		Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
		Expressed in kernel	Under Zn deficient condition	(Mondal *et al*., (2013)
		Might contribute to biofortification of maize		(Mondal *et al*., (2013)

	ZmZIP 6	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal et al., (2013))
		Expressed in kernel	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 7	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP8	Induced in shoot	Under Zn deficient condition	(Li *et al*., (2013)
		Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
		Expressed in kernel	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 9	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 10	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
	ZmZIP 11	Highly expressed in flag leaf	Under Zn deficient condition	(Mondal *et al*., (2013)
		Expressed in kernel	Under Zn deficient condition	(Mondal *et al*.,(2013)
	ZmZIP 12			
Wheat	TaZIP 3	Expressed in shoot and root	Under Zn starvation	(Evens *et al*., (2017)
	TaZIP 5	Expressed in shoot and root	Under Zn starvation	(Evens *et a*l., (2017)
	TaZIP 6	Expressed in shoot and root	Under Zn starvation	(Evens *et a*l., (2017)
	TaZIP 7	Expressed in shoot and root	Under Zn starvation	(Evens *et al*.,(2017)
	TaZIP 10	Expressed in flag leaf during grain development	-	(Deshpande *et al*., (2018)
	TaZIP 13	Expressed in shoot and root	Under Zn starvation	(Evens *et al*., (2017)
Barley	HvZIP 2	Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 3	Expressed in roots	Under Zn deficient condition	(Pedas *et al*., (2009)
		Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 5	Expressed in roots	Under Zn deficient condition	(Pedas *et al*., (2009)
		Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 7	Expressed in the vascular tissues of roots and leaves	Under Zn deficient condition	(Tiong *et al*., (2014)
		Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 8	Expressed in roots	Under Zn deficient condition	(Pedas *et al*., (2009)
		Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 10	Expressed in roots	Under Zn deficient condition	(Tiong *et al*., (2015)
		Expressed in shoots	Under Zn deficient condition	(Tiong *et al*., (2014)
	HvZIP 13	Expressed in roots	Under Zn deficient condition	(Tiong *et al*., (2015)
		Expressed in shoots	Under Zn deficient condition	(Tiong et al., (2014)
Foxtail millet	SiZIP 1	Moderately expressed in root, shoot and spica and less expressed in leaf		(Alagarasan *et al*., (2017)
	SiZIP 2	Highly expressed in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)
	SiZIP 3	Highly expressed in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)
	SiZIP 4	Highly expressed in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)
	SiZIP 5	Highly expressed in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)
	SiZIP 6	Comparatively low level of expression in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)
	SiZIP 7	Expressed in root, leaf, stem and spica.		(Alagarasan *et al*., (2017)

5. RICE

Sixteen ZIP transporter genes have been characterized in rice, although their role in the zinc transport system remains incompletely understood. Among these, OsZIP1, OsZIP3, OsZIP4, OsZIP5, OsZIP7, and OsZIP8 have demonstrated activity in zinc uptake and transportation from roots to shoots, including translocation into grains (Chen *et al*., 2008) (Bashir et al., 2012; Ishimaru et al., 2005; Ishimaru et al., 2006; Ishimaru et al., 2011; Lee & An, 2009; Lee et al., 2010; Lee et al., 2010; Meng et al., 2018; Ramesh et al., 2003). Expression of certain OsZIP genes varies across different plant parts, particularly under zinc deficiency. OsZIP4 exhibits heightened expression in nodal regions under zinc deficiency, while OsZIP3 shows activity in both roots and leaves under both sufficient and deficient zinc conditions. OsZIP7 and OsZIP8 are expressed in roots and shoots specifically under zinc-deficient conditions. Additionally, OsZIP4, OsZIP5, OsZIP6, and OsZIP7 share similarities with OsIRT1, with OsIRT1 displaying higher expression than OsIRT2 under iron deficiency. Functional impacts include the overexpression of OsIRT1 affecting tiller number and yield, while RNA interference of OsZIP1 leads to increased metal accumulation levels in roots. OsZIP9 plays a crucial role in zinc uptake from soil, showing high expression in lateral root cells under zinc deficiency. Knockout of OsZIP9 results in reduced zinc levels in shoots, roots, and grains under deficient zinc conditions, affirming its significance in zinc uptake. These findings collectively contribute to a deeper understanding of the involvement of ZIP transporter genes in zinc uptake and translocation within rice plants, particularly under conditions of zinc deficiency (Mohammed et al., 2022). various ZIP genes, along with their characteristics and the times of their expression as reported by different authors, are provided in Table 1.

6. MAIZE

In the maize genome, Li *et al*., (2013) identified eight ZIP transporters (ZmZIP1–ZmZIP8) and concluded that all the eight ZIP proteins were localized in plasma membrane. Similarly, Mondal *et al*., (2013) identified twelve ZIP transporters (ZmZIP1–ZmZIP8) in the maize genome. Out of which ten ZIP genes (ZmZIP1, ZmZIP2, ZmZIP4, ZmZIP5, ZmZIP6, ZmZIP7, ZmZIP8, ZmZIP9, ZmZIP10, ZmZIP11) are tissue specific and are expressed in flag leaf except for ZmZIP3 and ZmZIP12, under Zn deficient condition. Detailed characteristics of ZmZIP genes are given in Table 1.

7. WHEAT

In the wheat genome, Evens *et al.,* (2017) identified 14 TaZIP genes in bread wheat (*Triticum aestivum*) and analysed 5 ZIP genes (TaZIP3, TaZIP5, TaZIP6, TaZIP7, and TaZIP13) for the expression level in shoot and root under Zn starvation. All five genes showed increased expression in shoot and TaZIP3, TaZIP5, TaZIP7, and TaZIP13 showed increased expression in roots under Zn starvation conditions at different time. Similarly, Deshpande et al., (2018) analysed five ZIP genes and concluded that expression level of TdZIP1, TdZIP3, and TdZIP7 decreased in flag leaf and expression level of TdZIP10 and TdZIP15 increased in grain development.

8. BARLEY

In barley genome, Tiong *et al.,* (2015) identified thirteen HvZIP genes and studied their tissue specific expression under Zn deficiency condition. Six genes (HvZIP3, HvZIP5, HvZIP7, HvZIP8, HvZIP10, and HvZIP13) out of thirteen HvZIP genes were highly expressed under Zn deficient condition compared to Zn sufficient condition. Detailed descriptions of each HvZIP genes given by different authors are given in Table 1.

9. FOXTAIL MILLET

In foxtail millet genome, Alagarasan *et al.,* (2017) identified seven SiZIP genes (SiZIP1–SiZIP7) and analysed for the expression levels in root, leaf, stem and spica tissues of foxtail millet under drought stress conditions. Concluded that biofortification of Zn in foxtail millet could be achieved by using the highly induced SiZIP2, SiZIP3, SiZIP4, and SiZIP5 genes.

10. CONCLUSION

In conclusion, ZIP family transporters play vital roles in zinc uptake and transport within plants, contributing to Zn homeostasis and grain accumulation. The identification and characterization of ZIP transporter genes in various crops, including rice, maize, wheat, barley, and foxtail millet, provide valuable insights into their functions under different physiological conditions, particularly Zn deficiency (Krishna et al., 2020). Manipulating the expression of ZIP transporter genes holds promise for biofortification strategies aimed at enhancing Zn content in crops, thereby improving human nutrition and addressing global zinc deficiency challenges (Stanton et al., 2022). Future research efforts should focus on elucidating the regulatory mechanisms governing ZIP transporter expression and function, as well as exploring novel biotechnological approaches for optimizing Zn uptake and accumulation in crops to ensure food security and nutritional quality.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

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Details of the AI usage are given below:

1. Name: ChatGPT, VERSION 4.O
2. Source: OpenAI
3. Input prompts- Check the grammatical mistake was used

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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