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Genome-Wide Identification of Transition Metal Ion Transporters in *Oryza sativa*

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Abstract

Transition metals are essential minerals required for normal growth and development of plants which are taken in correct proportions from the soil and distributed throughout the plant. The concentrations of transition metals in roots, shoots and grains were analyzed in *Oryza sativa* indica cultivars viz., Sona Masuri (BPT 5204), Swarna (MTU 7029) and Vijetha (MTU1001). In roots the concentration of iron was highest in Sona masuri variety, followed by manganese and zinc. In shoots and grains, iron was highest followed by zinc suggesting specific transport mechanisms in all the parts. A total of 55 genes for transition metal ion transport were identified using *insilico* tools of which 18 involved in zinc/iron transport, 13 for copper, 7 for manganese, 3 for cobalt, 4 for cadmium and 10 transport metal ions belonging to Nramp family. Research carried out on these metal transporters mainly provides insights into the field of rice metal biology.

Keywords: *Oryza sativa*; Transition metals; ZIP family; Iron transporters; Zinc transporters

Introduction

Genome wide studies of the major cereals, including rice is being promoted world-wide in order to provide necessary impetus for substantial increase in production with increasing demand for food supplies [1]. The first rice genome sequence made accessible was that of the *O. sativa* sub sp japonica cv Nipponbare generated by the International Rice Genome Sequencing Project [2]. Andhra Pradesh is the fifth largest state in India where rice is the principal food crop cultivated throughout the state providing food for its growing population.

Transition metals are required for normal growth and development of plants which need to be carefully taken up in correct proportions from the soil through roots and be distributed throughout the plant and properly regulated to maintain homeostasis [3]. The complete catalog of 65 genes involved in transport of metal ions in *Neurospora crassa* were identified using *insilico* approaches [4]. This type of study was further substantiated by wet lab techniques wherein the copper transporters [5] and Nickel transporter [6] were transporting their respective metal ions in *N. crassa*.

Zinc (Zn), an essential nutrient in cells, plays a vital role in controlling cellular processes such as growth, development and differentiation. Five ZIP transporter genes have been reported for rice-OsIRT1, OsIRT2, OsZIP1, OsZIP3, and OsZIP4. OsIRT1 and OsIRT2 are ferrous iron transporters [7]. OsZIP1 is primarily associated with metal uptake and OsZIP3 with overall Zn homeostasis in the cell, especially in leaves [8].

The Nramps (Natural resistance associated macrophage proteins) are involved in metal ion transport of manganese and iron. In plants, this family was first identified in rice where three Nramps (OsNramp 1-3) were reported [9]. Till date, very little is known about the molecular mechanisms involved in transition metal transport across cell membranes in rice plant. The present work gives more emphasis on the presence of transition metal ion concentrations in three different plant varieties (BPT5204, MTU7029 and MTU1001) and identification of various metal transporter genes and their role involved in the distribution and uptake of these metal ions in *O. sativa* with the help of an array of *insilico* tools.

Materials and Methods**Rice varieties used**

Sona Masuri (BPT 5204) is one of the fine-grain variety of rice of 150 days duration with an average yield of 6tons/ha grown largely in various parts of Andhra Pradesh. Swarna (MTU 7029) is a semi-dwarf variety of 150 days duration with an average yield of 2.6 tons/ha which can be grown in saline soils. Vijetha (MTU 1001) is a fine variety of grain with 140 days duration, with an average yield of 2.4 tons/ha.

Estimation of metal content in rice plants

The three different rice varieties namely Sona masuri, Swarna and Vijetha were taken and metal content was estimated in roots, shoots and grains during initial and final stages of growth. Metal content of different plant samples (0.5 gms) were determined by subjecting it to wet acid digestion as described by Venkateswarulu and Sastry [10]. 5 ml of concentrated nitric acid and 1 ml of 70% perchloric acid are taken into a 50 ml conical flask, slowly heated to dryness on a sand bath. The residue was further digested with a 1:1 mixture of nitric acid and hydrochloric acid (5 ml) and finally with 10 ml hydrochloric acid. The final residue was dissolved in a suitable volume of deionized distilled water and metal ions estimated by Atomic Absorption Spectrometer (AAS:GBC-932 plus). Data shown are mean values of triplicates from two separate experiments (\pm SD).

Compilation of catalogue

Transport database, a relational database of a predicted cytoplasmic membrane transport protein complement for organisms was used for building a catalogue of transition metal transporter genes. For the

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identification of additional proteins, BLAST (Basic Local Alignment Search Tool) program [11], was used with functionally characterized prototype proteins of the other organisms. BLASTP hits are filtered according to high scoring pair algorithm in which each hit confronted by the query was evaluated by how they cover the reference protein. The “query coverage” extends over at least 30% of the reference protein identity is present, in the obtained hits than the hit is retained. The non-redundant protein database from Genbank was used to find out the closest known homologue among all organisms. Open reading frames are identified in the *O. sativa* genome were BLAST searched against SWISSPROT/TrEMBL database and only functionally characterized proteins in the database were taken into account for assigning predicted role to the proteins encoded by genes in the *O. sativa* genome. The sub-cellular localization of the proteins was predicted using TargetP server. Pfam domain search was carried out with the retrieved homologs, using Pfam database.

Phylogenetic analysis

It was performed using CLC’s combined workbench. For this analysis, multiple sequence alignment (MSA) was produced using progressive alignment algorithm [12]. The generated pair-wise alignments were used for finding the evolutionary distance between related transporter genes. Pair wise distances thus calculated were used to create a phylogenetic tree employing un weighted pair group method with arithmetic mean (UPGMA) algorithm with 1000 bootstrap replicates. After this analysis all the properties were merged and final table of transition metal transporters in *O. sativa* was formatted and annotated.

Results and Discussion

Metal ion concentration at different stages of *Oryza sativa*

The most commonly consumed three plant varieties (BPT5204, MTU7029, MTU1001) of *Oryza sativa* were taken. Root, shoot samples were taken at two different stages (Initial and final) of growth and individually subjected to acid digestion, it was observed that in roots, in both the stages (initial & final) the concentration of the metal ion iron was found to be highest in the Sona masuri (BPT5204) variety among all the transition metals considered, followed by manganese and zinc as shown in Figures 1a and 1b. The concentrations of other metals such as cobalt, cadmium and copper were found to be low (Figures 1a and 1b). In comparison to Sona masuri the other two varieties have much lower concentrations of all the transition metals suggesting that it has better gene expression systems rather than the other two (Figures 1a and 1b).

In shoots also, the metal ion concentration of the iron was found to be highest at all stages of growth followed by zinc that has been transported in higher quantities (Figures 2a and 2b). Manganese was transported in medium concentrations and cobalt, cadmium and copper in lower concentrations.

In grains also the highest metal concentrations were observed in the sona masuri rice variety as shown in Figure 3. The grains were more fortified with iron and zinc than the other transition metal ions. The concentration of manganese was decreased indicating less transport of manganese to grains. There is no significant increase or decrease in the concentrations of other elements like cadmium, copper and cobalt and these were transported in lesser concentrations (Figure 3).

Basic features of transition metal ion transporters of *Oryza sativa*

Plants require a range of transition metals as essential micronutrients

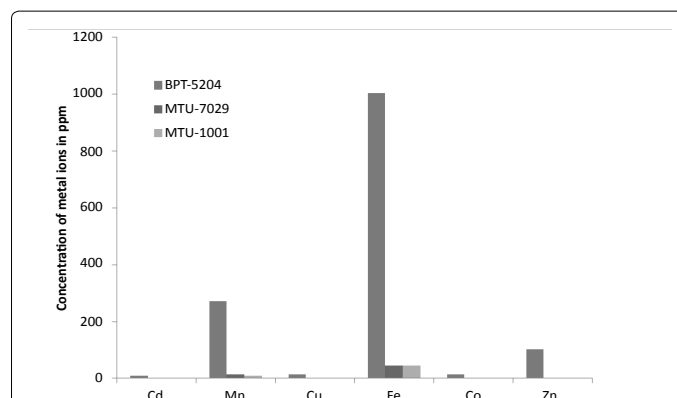


Figure 1a: The three rice plant varieties were taken and roots at initial and final stages were subjected to acid digestion and then analyzed using AAS and the metal ions concentrations were noted down. The data shown are mean values of triplicates from two separate experiments (\pm SD). a: Concentration of metal ions in initial stages of roots in three plant varieties of *Oryza sativa*.

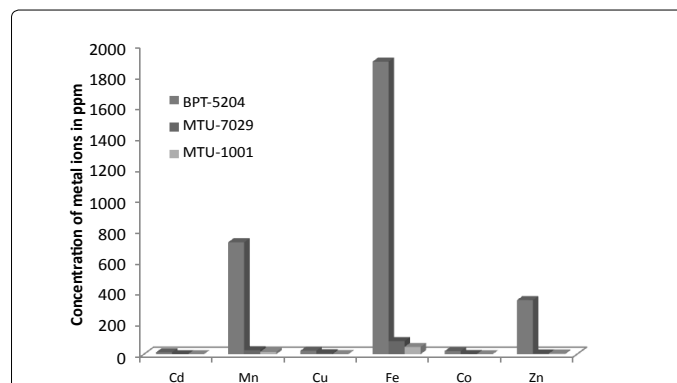
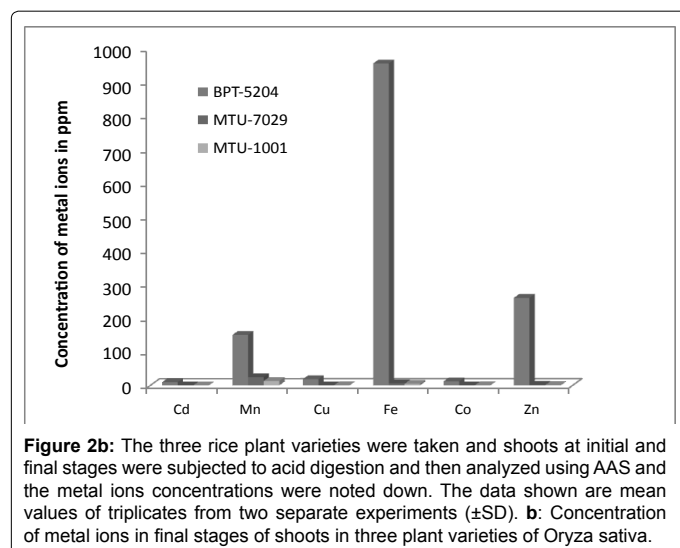
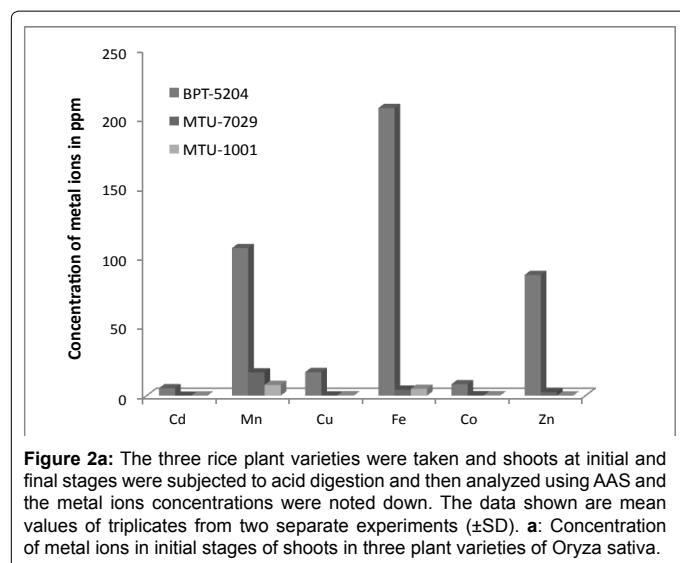


Figure 1b: The three rice plant varieties were taken and roots at initial and final stages were subjected to acid digestion and then analyzed using AAS and the metal ions concentrations were noted down. The data shown are mean values of triplicates from two separate experiments (\pm SD). b: Concentration of metal ions in final stages of roots in three plant varieties of *Oryza sativa*.

for normal growth and development. These transition metal transport system consists of both high and low affinity transporters to maintain the homeostasis in either metal deplete or replete conditions. Some of the transition metals include zinc, iron, cadmium, manganese, copper, cobalt. A complete catalogue of 55 genes with a putative role in transition metal homeostasis of *O. sativa* were identified and summarized in Table 1. The data presented in table 1 indicated that the transporters for the transition metal zinc outnumbered the rest of the metal ion transporters. Out of 55 transporters only 15 transporters belonging to different families have been identified. Remaining 40 transporters may also play a crucial role in maintaining the homeostasis of different transition metal ions in rice plant.

Zinc transport: Zinc plays many essential and unique biological roles because of its unique chemical characteristics. It is well known that a vast array of proteins use zinc for stabilizing their structures in a functional form [13]. To understand zinc transport in rice, we identified putative zinc transporters in gene databases. *O. sativa* consists of 18 members belonging to ZIP family that are likely to be involved in zinc uptake as shown in Table 1. Of the 18, five zinc transporters are already characteristics stating their role in zinc transport in rice. The



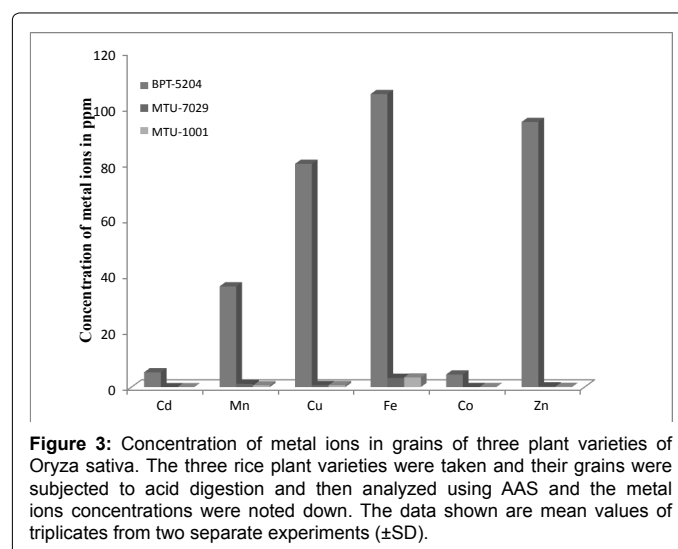
expression patterns of OsZIP1, OsZIP3, and OsZIP4, which encode Zn transporters in rice, were studied and OsZIP1 was expressed only in the roots and very weakly in the panicles, while the other two genes were expressed in all parts of the plant. The Zn-deficient conditions up-regulated the expression of OsZIP1, OsZIP3, and OsZIP4 in the roots and that of OsZIP4 in the shoots indicating that all these genes participate in rice zinc nutrition [14]. OsZIP5, which is inducible under Zn deficiency, has complemented the growth defect of a yeast Zn-uptake mutant, indicating that it is a Zn transporter localized to the plasma membrane and plays a role in Zn distribution within rice [15].

ZIP family was split into several subfamilies based on a higher degree of sequence conservation within these groups that include LIV-1, ZIP I and ZIP II. ZIP I consists largely of plant and fungal members whereas sub family II is a smaller group of mammalian and nematode proteins. Phylogenetic analysis as shown in Figure 4 predicted two members to be grouped under ZIP I sub-family, eleven in ZIP II family and one in LIV-1 family. One member (Os01g74110) is homologous to ZIP I of *Oryza sativa* that is mainly induced by zinc or iron depletion [16]. Similarly another member (Os5g10940) is homologous to the zinc transporter 4 in *Zea mays* which is also helpful in the uptake of zinc.

Zinc transporters are more prevalent in ZIP I family but the presence of these transporters in ZIP II family also suggests adaptive mechanisms by these plants for zinc and iron fortification (Figure 4). A comparison of the protein sequences and ionic selectivity suggests that all these transporters may play different roles in the physiology of the whole plant.

Iron transport: Iron is the most versatile transition metal ion in biological redox reactions. Decades of research on plants have established that there are two distinct iron uptake systems based on the response of plants to iron deficiency. Strategy I plants (dicots and non-graminaceous monocots) respond to Fe deficiency by decreasing rhizosphere pH and reducing sparingly soluble ferric iron. Strategy II plant (graminaceous monocots) have iron uptake systems that release mugineic acid- family phytosiderophores to the rhizosphere, where they solubilize sparingly soluble iron by chelation. The chelated complex is then absorbed by the roots. It is believed that plants utilize any one of these strategies but the first iron transporter identified in rice plant was OsIRT1 [17]. In this study the metal analysis showed more amount of iron acquisition in roots, shoots and grains which may be due to the presence of more number of Zn/Fe transporters that may be quite selective only for iron. Not only are these, citrate transporters (OsFRDL1) also reported to transport iron in rice [18]. Apart from this, grains have shown comparatively more amount of iron accumulation (Figure 3) when compared with other transition metals. This has far reaching consequence and implications for nutritional security. Further the wet lab work of these Zn/Fe transporters will help in understanding the transport process of this essential trace element.

Copper transport: Copper is an essential trace element required for many enzymes and proteins involved in various biological processes such as protection against oxidative stress, normal cell growth and development. A Copper Transporter family (Ctr) member carries out copper uptake in lower to higher eukaryotes. The copper (Cu) transporter (COPT/Ctr) gene family has an important role in the maintenance of Cu homeostasis in different species. The Ctr proteins were first identified in *Saccharomyces cerevisiae* and later it served as a powerful tool for identification of several copper transporter proteins in other fungi, flies, plants and mammals. The characteristic features of these Ctr family members are the presence of two or three transmembrane domains, MXXM and MXM motifs in amino terminal regions, conserved cysteine and histidine residues in carboxy terminus



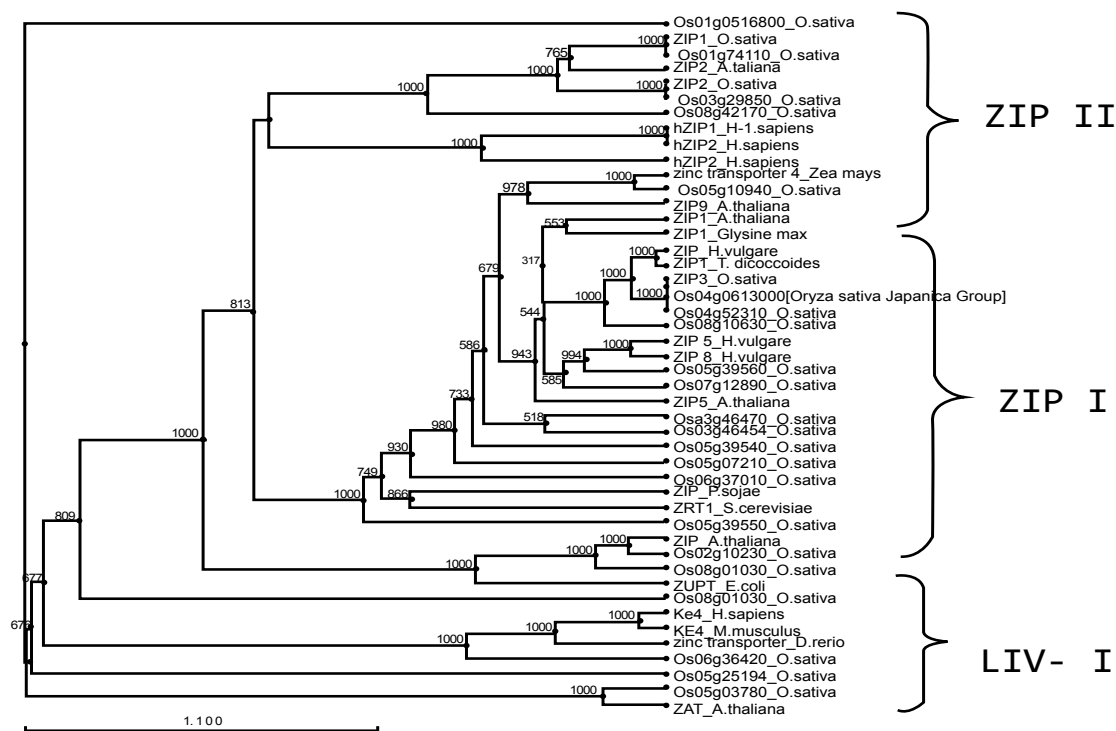


Figure 4: Phylogenetic tree of Zn^{2+} transporters. Bootstrap values are indicated on the branch points. A.thaliana- Arabidopsis thaliana; O.sativa- Oryza sativa; D.reio- Danio rerio; M.musculus- Mus musculus; S.cerevisiae- Saccharomyces cerevisiae; E.coli- Escherichia coli; H.vulgare- Hordeum vulgare; H.sapiens- Homo sapiens; T.dicoccoides- Triticum dicoccoides; P.sojae- Phytophthora sojae.

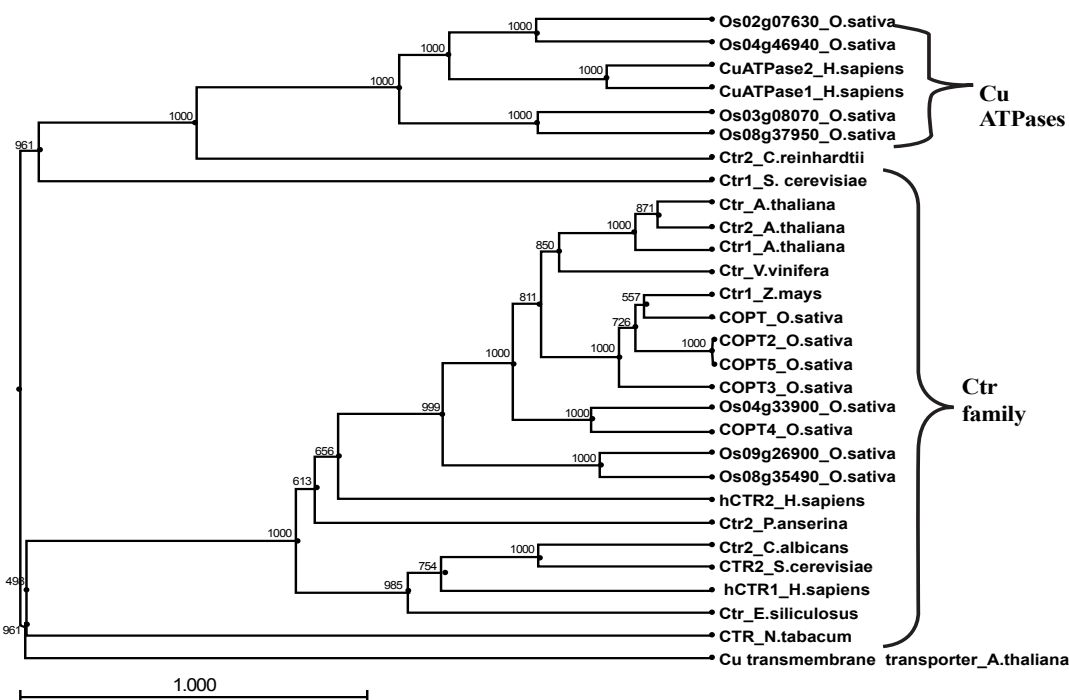
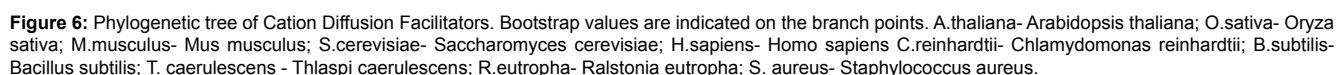


Figure 5: Phylogenetic tree of Cu^{2+} transporters and Cu^{2+} - ATPases. Bootstrap values are indicated on the branch points. A.thaliana- Arabidopsis thaliana; O.sativa- Oryza sativa; M.musculus- Mus musculus; S.cerevisiae- Saccharomyces cerevisiae; H.sapiens- Homo sapiens; N.tabacum- Nicotiana tabacum; E.siliculosus- Ectocarpus siliculosus; Z.mays- Zea mays; V.vinifera- Vitis vinifera; M.truncatula- Medicago truncatula; C.albicans- Candida albicans; P.anserina- Podospora anserina; C.reinhardtii- Chlamydomonas reinhardtii.

be considered to transport zinc or cadmium. It is also supported by the fact that Cd accumulation is mediated by ability of root-to-shoot Cd translocation via the xylem and is the major physiological process that determines the accumulation in shoots and grains in rice plants [21].

Manganese transport: Manganese is another essential micronutrient that is required for the growth. Nramp (Natural resistance-associated macrophage proteins) represents a large family of metal transporters that are well conserved from bacteria to mammals that play an important role in transport of iron and manganese [22]. Seven members are identified in *Oryza sativa* that belong to this group and hence they are assumed to transport manganese (Table 1). In plants, this family was first identified in rice where three Nramps (*OsNramp 1-3*) were reported. Expression studies in normal plant tissues indicate that *OsNramp1* is expressed primarily in roots, while *OsNramp2* is primarily expressed in leaves and *OsNramp3* is expressed in both tissues [8]. Apart from these seven, having ion selectivity for manganese there are still ten other transporters belonging to this family that may transport manganese. This might be the reason for accumulation of more amount of this metal ion in root, shoot and grains next to iron as shown in Figures 1-3. Clearly, the possibility of *Nramp* homologues that are implicated in metal transport pathway in plants need to be addressed in a series of plant mutants lacking one or all of the identified *OsNramp* genes to get a clear picture of its transport.

Nickel/Cobalt transport: Nickel is an essential component of metalloenzymes involved in energy and nitrogen metabolism. Accumulation of nickel is dependent on high affinity uptake of this metal ion from natural environments where they are available only in trace amounts. Cobalt is now recognized as a trace element and is an essential component of many enzymes [23]. NiCoT is the family that



Gene ID	Family Name	Specificity	Cellular Location	Tissue Expression
Os01g56400	ABC Family	Cd	Cytoplasm	Roots/Shoots
Os11g29850	ABC Family	Cd	Endoplasmic reticulum	Roots/Shoots
Os05g33230	ABC Family	Co	Plasma membrane	Roots/Shoots
Os05g03780	CDF Family	Zn/Cd	Chloroplast thylakoid membrane	Leaves
Os08g32650	CDF Family	Zn/Cd	Plasma membrane	Roots/Shoots
OsZIP1	ZIP Family	Zn	Plasma membrane	Roots
Os02g10230	ZIP Family	Zn	Plasma membrane	Roots/Shoots
Os03g29850	ZIP Family	Zn	Chloroplast thylakoid membrane	Leaves
Os03g46454	ZIP Family	Zn/Fe	Mitochondrial inner membrane	Roots/Shoots
OsIRT1	ZIP Family	Fe	Plasma membrane	Roots
OsZIP3	ZIP Family	Zn/Fe	Plasma membrane	Roots
OsZIP6	ZIP Family	Zn/Fe	Chloroplast thylakoid membrane	Leaves
OsZIP7	ZIP Family	Zn	Plasma membrane	Shoots
Os05g25194	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os05g39540	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os05g39550	ZIP Family	Zn/Fe	Mitochondrial inner membrane	Roots/Shoots
OsZIP5	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os06g37010	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os07g12890	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os08g01030	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
OsZIP4	ZIP Family	Zn/Fe	Plasma membrane	Shoots
Os08g36420	ZIP Family	Zn/Fe	Plasma membrane	Roots/Shoots
Os08g42170	ZIP Family	Zn	Plasma membrane	Roots/Shoots
Os02g07630	P-ATPase Family	Cu	Plasma membrane	Roots/Shoots
Os02g10290	P-ATPase Family	Cu	Plasma membrane	Roots/Shoots
Os03g08070	P-ATPase Family	Cu	Plasma membrane	Roots/Shoots
Os04g46940	P-ATPase Family	Cu	Plasma membrane	Roots/Shoots
Os08g37950	P-ATPase family	Cu	Chloroplast	Leaves
OsCOPT1	Ctr Family	Cu	Plasma membrane	Leaves/Shoots
OsCOPT3	Ctr Family	Cu	Plasma membrane	Leaves/Shoots
OsCOPT4	Ctr Family	Cu	Nucleus	Leaves
Os04g33900	Ctr Family	Cu	Plasma membrane	Roots/Shoots
OsCOPT2	Ctr Family	Cu	Plasma membrane	Leaves/Shoots
Os08g35490	Ctr Family	Cu	Plasma membrane	Roots/Shoots
Os09g26900	Ctr Family	Cu	Plasma membrane	Roots/Shoots
OsCOPT5	Ctr Family	Cu	Plasma membrane	Leaves/Shoots
Os03g06090	Ni-CoT Family	Ni/Co	Plasma membrane	Roots/Shoots
Os06g02580	Ni-CoT Family	Ni/Co	Plasma membrane	Roots/Shoots
Os3g49400	Nramp Family	Mn	Plasma membrane	Roots/Shoots
Os07g06130	Nramp Family	Mn	Plasma membrane	Roots/Shoots
Os07g06190	Nramp Family	Mn	Endoplasmic reticulum	Roots/Shoots
Os07g06300	Nramp Family	Mn	Endoplasmic reticulum	Roots/Shoots
OsNramp1	Nramp Family	Mn	Plasma membrane	Roots
OsNramp2	Nramp Family	Mn	Chloroplast	Leaves
OsNramp3	Nramp Family	Mn	Plasma membrane	Roots/Shoots
Os01g31870	Nramp Family	Me	Plasma membrane	Roots/Shoots
Os01g53210	Nramp Family	Me	Chloroplast	Leaves
Os02g03900	Nramp Family	Me	Plasma membrane	Roots/Shoots
Os03g41064	Nramp Family	Me	Nucleus	Roots/Shoots
Os03g41070	Nramp Family	Me	Chloroplast	Leaves
Os07g15370	Nramp Family	Me	Plasma membrane	Roots/Shoots
Os02g39180	Nramp Family	Me	Plasma membrane	Roots/Shoots
Os03g49400	Nramp Family	Me	Nucleus	Roots/Shoots
Os07g06130	Nramp Family	Me	Plasma membrane	Roots/Shoots
Os07g06190	Nramp Family	Me	Chloroplast	Leaves

Table 1: Summary of transition metal ion transporters in *Oryza sativa*.

is useful for the transportation of Ni/Co metal and it has a conserved signature sequence (RHALDADHI) which is the characteristic feature

of this family. There are two members identified in *Oryza sativa* that belong to this family which are considered to transport Nickel/Cobalt.

One member belongs to ABC family which has more specificity to cobalt. However till date the importance of either Ni²⁺ or Co²⁺ in *O. sativa* metabolism has not been understood.

Conclusion

Research carried out on these metal transporters mainly provides insights into the field of rice metal biology. This study helps in figuring out the regulatory networks of metal transporters and assembling the complete picture of transition metal homeostasis. These appealing hypotheses need to be tested experimentally. Quantification of metals in rice tissues experimentally, supports Sona masuri (BPT5204) to be a promising variety both in yield and nutrition with respect to metal ions. The recent advances in biochemical, molecular and genetic techniques including the rapidly expanding use of microarrays and gene knockouts, will definitely help in defining more clearly the specificity, location, regulation and physiological role of these transition metal transporters particularly in plants pertaining to food crops and thereby influence the economy and food security of the nation.

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