

# The Uptake and Translocation of Zinc in Graminaceous Plants

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## INTRODUCTION

Zinc is an essential nutrient that plays important roles in numerous physiological processes in plants, serving as a cofactor for many enzymes and as the key structural motifs in transcriptional regulatory proteins. A deficiency of Zn decreases growth, but excess-Zn is toxic to biological systems through metal-based cytotoxic reactions. Therefore, the uptake and transport of Zn must be strictly regulated. Intracellular Zn homeostasis is achieved through the coordinated regulation of specific transporters engaged in Zn influx, efflux, and intracellular compartmentalization.

The uptake and translocation of mineral nutrients in plants is essential for plant growth, and since plants are the primary source of food for humans, the nutritional value of plants is of central importance to human health. Over 50% of the world populations suffer from micronutrient deficiency. Iron and Zn deficiencies are especially prevalent nutritional disorder in humans. Increasing the ability of plants to provide higher Zn levels will have a dramatic impact on human health. Increasing the Zn uptake from soils is one prerequisite to increase the amount of Zn in edible parts of plants. This can be aided by identifying the transporters involved in the translocation of Zn within plants.

## RESULTS AND DISCUSSION

### ZIP family Transporters in Rice Plants

The ZIP family (Zn-regulated transporter/Fe-regulated transporter-like protein) transporters are thought to be responsible for the uptake of divalent metals, including Zn, into the roots of graminaceous and non-graminaceous plants. Rice possesses 12 putative ZIP transporters. Previously, Ramesh et al (2003) reported that OsZIP1 and OsZIP3 were involved in Zn transport in rice.

We isolated *OsZIP4* that exhibits sequence similarity to the ferrous ion transporter in rice, *OsIRT1*. Northern blot analysis revealed that *OsZIP4* was highly expressed under conditions of Zn deficiency in roots and shoots. Therefore, the expression of *OsZIP4* was regulated by the Zn status of the plant. The *OsZIP4* transcripts were more abundant than those of *OsZIP1* and *OsZIP3*. The *OsZIP4* complemented a Zn-uptake-deficient yeast (*Saccharomyces cerevisiae*) mutant,  $\Delta zrt1\Delta zrt2$ , indicating that *OsZIP4* is a functional transporter of Zn. The *OsZIP4*-sGFP fusion protein was transiently expressed in onion epidermal cells localized to the plasma membrane. *In situ* hybridization analysis revealed that *OsZIP4* in Zn-deficient rice was expressed in the meristem of Zn-deficient roots and shoots, and in phloem cells of roots and shoots. These results suggested that *OsZIP4* is a functional Zn transporter that may be responsible for the translocation of Zn within rice plants. Interestingly, *OsZIP4* is also strongly expressed in both root and shoot apical meristems, where the strong requirement of Zn in cell division would cause *OsZIP4* expression

### **Contribution of MAs to Zn uptake**

Graminaceous plants produce and secrete mugineic acid family phytosiderophores (MAs) to acquire Fe from the rhizosphere. In addition to Fe(III), MAs chelate various divalent cations, including Zn(II). Although Zn has been thought to be taken up mainly as free Zn<sup>2+</sup> ions, the uptake of Zn(II)-MAs complexes has also been proposed. We showed increased expression of the genes that participate in the biosynthesis and increased secretion of MAs in Zn-deficient barley. Moreover, an analysis using the positron-emitting tracer imaging system (PETIS) confirmed that Zn-deficient barley absorbs Zn(II)-MAs and free Zn<sup>2+</sup> ions with higher uptake rates observed for Zn(II)-MAs. However, in rice, the secretion of MAs decreases under Zn deficiency. A PETIS experiment also showed that Zn-deficient rice plants absorb lower amounts of Zn when supplied with MAs, suggesting a relatively low contribution of MAs to Zn uptake in rice.

In all higher plants, nicotianamine (NA) is thought to be one of the principal metal chelators, including Fe and Zn. In addition to the central role of NA, MAs synthesized by graminaceous plants are thought to be involved in Fe and Zn translocation.

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