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, therefore, decreases growth, but excess Zn has significant toxicity 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 inorganic nutrients 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 population suffers from micronutrient deficiency. Iron and Zn deficiency are especially prevalent nutritional disorder in humans. Increasing the ability of plants to provide higher levels Zn, will have a dramatic impact on human health. Increasing the Zn uptake from soils is a prerequisite to increase the amount of Zn in the edible parts of plants. This can be aided by identifying the transporters involved in the translocation of Zn in 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, in 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 exhibited a sequence similarity to the rice ferrous ion transporter, *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 plant's Zn status. The *OsZIP4* transcripts were more abundant than transcripts of *OsZIP1* and *OsZIP3*. The OsZIP4 complemented a Zn-uptake-deficient yeast (*Saccharomyces cerevisiae*) mutant, Δ*zrt1*Δ*zrt2*, indicating that OsZIP4 is a functional transporter of Zn. The OsZIP4-sGFP fusion protein was transiently expressed in onion epidermal cells localized at 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 suggest 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 root and shoot apical meristems, where the strong requirement of Zn in cell division would cause *OsZIP4* expression.

Contribution of Mugineic Acid Family Phytosiderophores 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^{2+} ions, the uptake of Zn(II)-MAs complexes has also been proposed as a possible uptake mechanism. We show increased expression of genes that participated 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 absorbed Zn(II)-MAs and Zn^{2+} ions, with higher uptake rates observed for Zn(II)-MAs. However, in rice, the secretion of MAs decreases under Zn deficiency. A PETIS experiment showed also that Zn-deficient rice plants absorbed 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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