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The rice *zebra3* (*z3*) mutation disrupts citrate distribution and produces transverse dark-green/green variegation in mature leaves

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[Introduction]

Rice *zebra* mutants are leaf variegation mutants that exhibit transverse sectors of green/yellow or green/white in developing or mature leaves. In most cases, leaf variegation is caused by defects in chloroplast biogenesis pathways, leading to an accumulation of reactive oxygen species in a transverse pattern in the leaves. Here, we examine a new type of leaf variegation mutant in rice, *zebra3* (*z3*), which exhibits transverse dark-green/green sectors in mature leaves and lacks the typical yellow or white sectors.

[Materials and Methods]

The *zebra3-1* (*z3-1*) mutant was isolated from a mutant pool produced by applying N-methyl-N-nitrosourea, to a japonica rice cultivar 'Kinmaze', as previously described (Iwata et al. 1979). All rice plants were grown under natural long day conditions (approximately 14 h light/day) in a paddy field (Suwon, Korea, 37°N latitude).

[Results and Discussions]

Map-based cloning revealed that the *Z3* locus encodes a putative citrate transporter that belongs to the citrate-metal hydrogen symport (CitMHS) family. CitMHS family members have been extensively studied in bacteria and function as secondary transporters that can transport metal-citrate complexes, but whether CitMHS family transporters exist in eukaryotes remains unknown. To investigate whether *Z3* acts as a citrate transporter in rice, we measured citrate levels in the wild-type leaves and in the dark-green and green sectors of the leaves of *z3* mutants. The results showed that citrates accumulated to high levels in the dark-green sectors of *z3* mutant leaves, but not in the green sectors as compared with the wild-type leaves. These results suggest that leaf variegation in the *z3* mutant is caused by an unbalanced accumulation of citrate in a transverse pattern in the leaves. Taking these results together, we propose that *Z3* plays an important role in citrate transport and distribution during leaf development and is a possible candidate for a CitMHS family member in plants.

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