

Introduction

Silicon (Si) is the second most prevalent element within the lithosphere (Exley 1998). Silicon shows various beneficial effects on plant growth and productivity by alleviating biotic and abiotic stresses (Ma and Yamaji 2006; 2008). These beneficial effects mostly results from the deposition of Si in their tissues (Ma 2004). However Si concentration of plant shoots varies widely (0.1% to 10% of Si in dry weight), depending on the plant species (Epstein 1994; Ma and Takahashi 2002).

Recently three Si transporters (OsLsi1, OsLsi2, and OsLsi6) have been identified from rice, which is a Si-accumulating species (Ma et al. 2006; Ma and Yamaji 2006; Ma et al. 2007; Yamaji et al. 2008). OsLsi1 and OsLsi2 are mainly expressed in roots and have Si influx and efflux transport activity, respectively. In contrast, OsLsi6 is mainly localized at distal side of xylem parenchyma cells in the rice leaf blade and showed Si influx transport activity. From these results, OsLsi1 and OsLsi2 are involved in Si uptake from roots, while OsLsi6 is responsible for the xylem loading (Yamaji et al. 2008).

In contrast to the progress that has been made in identification of Si transporters in rice, little is known on Si uptake and accumulation mechanism in the other crops. In this study, we identified three genes which are involved in Si uptake and xylem unloading in maize (*Zea mays* L. cv B73).

Results and Discussion

Maize takes up Si actively from the roots (Liang et al. 2006; Tamai and Ma 2003). We identified the Si transporter genes (*ZmLsi1*, *ZmLsi2*, and *ZmLsi6*) as homologues of rice Si transporters (Mitani et al. 2009). Each transporter shared more than 80% between maize and rice at amino acid level.

Similar to the rice silicon transporters, both Lsi1-like transporters *ZmLsi1* and *ZmLsi6* showed silicon influx transport activity (Fig. 1A), while *ZmLsi2* showed only efflux activity when they were expressed in *Xenopus laevis* oocyte (Fig. 1B). The mRNA of *ZmLsi1* and *ZmLsi2* was expressed mainly in the roots, while *ZmLsi6* was in both the root and the shoots. The expression of *ZmLsi1* and *ZmLsi6* in the roots was constitutive and was not affected by continuous supply of Si. In contrast, *ZmLsi2* expression was significantly decreased by Si supply. Immunostaining showed that *ZmLsi1* was polarly localized at the distal side of root epidermis, hypodermis and cortex cells, while *ZmLsi2* was only at the endodermis without polarity. *ZmLsi6* was localized at the xylem parenchyma cells in the leaf blades. Taken together, our results indicate that *ZmLsi1* and *ZmLsi2* are involved in the uptake of Si from the roots, while *ZmLsi6* is mainly responsible for the xylem unloading of Si in maize.

A previous study showed that the uptake capacity of Si by the roots is much higher in rice than in maize (Tamai and Ma, 2003). This difference may result from different localization and expression pattern of Si transporters between rice and maize although further works are required.

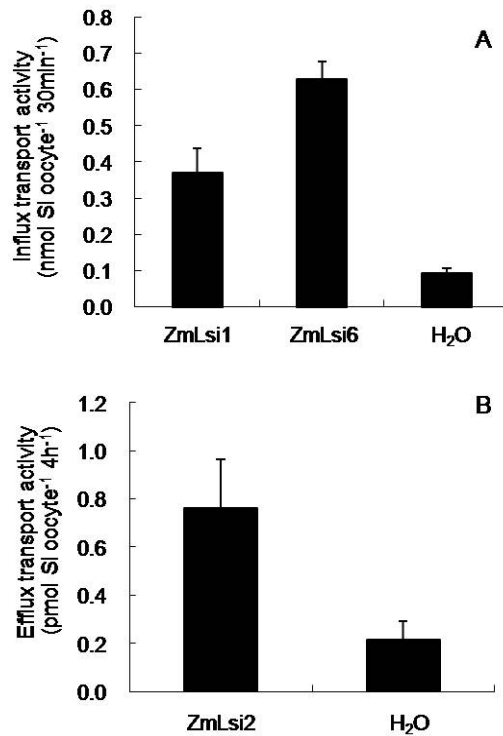


Fig. 1 Transport activity of ZmLsi1, ZmLsi6 and ZmLsi2 in *Xenopus laevis* oocytes. (A) Si influx transport activity of ZmLsi1 and ZmLsi6. (B) Si efflux transport activity of ZmLsi2. Values are means \pm SD of three replicates.

References

- Exley C. Silicon in life: A bioinorganic solution to bioorganic essentiality. *J. Inorg. Biochem.* 1998; 69: 139-144.
- Ma JF and Yamaji N. Silicon uptake and accumulation in higher plants. *Trends Plant Sci.* 2006; 11: 392-397.
- Ma JF and Yamaji N. Functions and transport of silicon in plants. *Cell. Mol. Life Sci.* 2008; 65: 3049-3057.
- Ma JF. Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. *Soil Sci. Plant Nutr.* 2004; 50: 11-18.
- Epstein E. The anatomy of silicon in plant biology. *Proc. Natl. Acad. Sci. U. S. A.* 1994; 91: 11-17.
- Ma JF and Takahashi E. *Soil, Fertilizer, and Plant Silicon Research in Japan*, Amsterdam: Elsevier Science; 2002.
- Ma JF, Tamai K, Yamaji N, Mitani N, Konishi S, Katsuhara M, Ishiguro M, Murata Y, Yano M. A silicon transporter in rice. *Nature* 2006; 440: 688-691.
- Ma JF, Yamaji N, Mitani N, Tamai K, Konishi S, Fujiwara T, Katsuhara M, Yano M. An efflux transporter of silicon in rice. *Nature* 2007; 448: 209-212.
- Yamaji N, Mitani N and Ma JF. A transporter regulating silicon distribution in rice shoots. *Plant Cell* 2008; 20: 1381-1389.
- Liang YC, Hua HX, Zhu YG, Zhang J, Cheng CM, Romheld V. Importance of plant species and external silicon concentration to active silicon uptake and transport. *New Phytol.* 2006; 172: 63-72.
- Tamai K and Ma JF. Characterization of silicon uptake by rice roots. *New Phytol.* 2003;

158: 431-436.

Mitani N, Yamaji N and Ma JF. Identification of maize silicon influx transporters. *Plant Cell Physiol.* 2009; 50: 5-12