Distribution pattern of silicon transporters in maize seedlings

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Abstract

The relationship between relative expression of three Si transporter (*Lsi1*, *Lsi2*, and *Lsi6*) genes and Si contents in four different segments of maize seedlings viz. basal, apical parts of seminal roots, leaf sheaths, and blades was investigated under Si concentrations (0, 2, and 10 mM). Results indicated that under the control conditions, Si contents in aerial parts and roots of seedlings were identical, but under 2 and 10 mM Si concentrations, its content in the aerial parts was higher than the roots. Silicon uptake by maize seedlings was not proportional to the increase in its supply. Unexpectedly, the Si content of maize seedlings did not increase when the Si supply increased to 10 mM. Results also showed that under normal conditions, relative expressions of *ZmLsi1* and *ZmLsi2* in shoots of maize seedlings were significantly higher than roots while *ZmLsi6 was* mainly expressed in leaf sheaths. Application of Si significantly increased all three silicon transporter expressions. Among these transporters, the response of Lsi2 was discriminative to the external Si concentration so that under 10 mM Si, the expression of Lsi2 was more noticeable. The results suggested that Lsi2 may have a role in efflux of Si in maize under high concentration of external Si.

Keywords: Lsi1, Lsi2, Lsi6, maize, seedling, silicon

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Introduction

Silicon (Si) is the most abundant element in the lithosphere after oxygen but generally remains in an undissolved form, where plants are unable to uptake (Souri et al., 2021). As of now, the function of Si in the plant metabolism is unknown. It has been well-documented however, that Si protects plants from various biotic and abiotic stresses. Deficiencies have also been documented to cause various abnormalities in a wide variety of plant species. This is why Si is usually referred as a "quasi-essential" nutrient (Ma and Yamaji, 2008).

In soils solution, Si is found in the form of monosilicic acid (H_4SiO_4) with concentrations of about 100-500 µM (Sommer et al., 2006). Therefore, all plants grown in soil will contain some Si in their tissues (Epstein et al., 1999; Ma and Takahashi, 2002; Hodson et al., 2005). However, the amount of silicon varies significantly in different plant species, ranging anywhere from 0.1% to 10% of dry weight. This is attributed to varying silicon uptake mechanisms in plant roots

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(Epstein et al., 1999). Three modes of Si uptake have been suggested, namely passive uptake by accumulators, active uptake by intermediate-types, and rejection for Si excluder plants (Debona et al., 2017). Also, some recent studies indicated that applying Si can improve the uptake of macro and micronutrients, especially in nutrient deficient conditions (Etesami and Jeong, 2018; Soratto et al., 2019).

Maize is an Si-accumulator bearing both passive (especially at high concentration of Si) and active uptake mechanisms (Liang et al., 2006). Three Si transporters, i.e., Lsi1, Lsi2, and Lsi6 have been recognized for the first time in rice and then in other plants. *ZmLsi1,* which is mainly expressed in maize roots, is homologous of *OsLsi1* of rice with 83% identity at amino acid level, has an open reading frame (ORF) that can be as long as 888 bps, and its deduced protein comprises of 295 amino acids. This influx transporter of Si is localized in distal side of root epidermal and hypodermal cells (Mitanti et al., 2009b). *ZmLsi2,* has 86% identity at amino acid level with *OsLsi2* and has a 1431 bps long ORF, encoding a 477 amino acids protein. *ZmLsi2* is a Si efflux transporter that is localized on the plasma membrane of the root endodermis cells, with no polarity (Mitanti et al., 2009a). *ZmLsi6* is the third known Si transporter in maize which is homologous of rice *OsLsi6* with 89% identity at amino acid level, and has an open reading frame (ORF) as long as 885bp that encodes a 294 amino acids protein. In contrast with *ZmLsi1* and *ZmLsi2, ZmLsi6* is mainly expressed in maize leaf blade and especially leaf sheaths in addition to roots (Mitani et al., 2009b). No polar localization of ZmLsi6 was observed in roots. In shoots, ZmLsi6 protein was only observed in the xylem parenchyma cells that are adjacent to the vessels in both leaf sheaths and leaf blades. ZmLsi6 in leaf sheaths and blades also exhibited polar localization on the side facing toward the vessel (Mitani et al., 2009b). The function of ZmLsi6 is likely the efflux of Si from stele to leaf blades (Yamaji et al., 2008).

Some literature is available about the innate expression pattern of Si transporter genes and their localization in different maize tissues. However, to the best of our knowledge, such studies have not yet been conducted under varying concentrations of Si. Therefore, the relative expression of the three Si transporter genes (*Lsi1*, *Lsi2,* and *Lsi6*) in different parts of maize seedlings (basal and apical region of seminal roots, and leaf sheaths and blades) under three Si concentrations (0, 2 and 10 mM Si) was subject of the present research. Any relationship between expression pattern of Si transporters in the examined parts and their Si content are discussed.

Materials and Methods

Plants materials

Maize (*Zea mays* var. merit) seeds were surface sterilized by sodium hypochlorite %10 (w/v), EtOH %70, and then thoroughly rinsed with deionized water. Then, the seeds were imbibed in sterile water for 12 h and were placed between two sheets of sterile filter paper moistened with 60 mL of 0.2 mM MES buffer, pH 5.2, and containing different concentrations of Si as $Na_2SiO_3.5H_2O$. The cellophane-covered containers were placed in a growth chamber at 25 ℃ with a relative humidity of 60% for the first three days in dark, and then in a 16 h photoperiod with a photosynthetic photon flux of 107 mmol m^{-2} s^{-1} (400–700 nm) at the plant level. The growth of seedlings was monitored for 12 days. Based on the results of the growth analysis, 2 mM and 10 mM of Si were respectively selected as the optimum and high concentrations for further trials. Expression pattern of Si transporter genes as well as the content of Si were evaluated in leaf blades, leaf sheaths, basal (20 mm distal zone), and apical parts (0-20 mm of the root tip) of seminal roots. The samples were dried at 90 ℃, turned into ash at 550 ℃ for 3.5 h, and dissolved in 2 mL H_2NO_3. The acidic extracts were dried on a sand bath and re-dissolved in hydrofluoric acid (HF, 40% v/v) before applying to atomic absorption spectrophotometry (Shimadzu AA-670, Kyoto, Japan).

RNA extraction and RT-PCR analysis

Total RNA was extracted using RNX plus TM kit according to manufacturers' instructions (Cinnagen, Tehran, Iran). The quality and integrity of the extracted RNA was examined by electrophoresis on a 1% agarose gel and staining with ethidium bromide. Two microgram of total

RNA was used for cDNA synthesis, using 1µg oligo-dT primer and 200 U RevertAidTM M-MuLV Reverse Transcriptase (Fermentas) in a 20 µl reaction and according to the manufacturer's instructions. Semi-quantitative RT-PCR technique was performed for detection of relative expression level of the three selected genes (*Lsi1*, *Lsi2*, and *Lsi6*) using 18S rRNA as an internal control with following primers:

ZmLsi1 forward: 5-ATCTACGCCGTCGGCCACATCTC-3´
ZmLsi1 reverse: 5-AGCTTGAAGGAGGAGAGCTTCTG-3´
ZmLsi2 forward: 5-TTCCACGTGATCAGCCCCGACGA-3´
ZmLsi2 reverse: 5-GAAGAAGACGAGCAGCGAGTAGG-3´
ZmLsi6 forward: 5-TCTACTACCCCGAGAAATCCTTCGC-3´
ZmLsi6 reverse: 5- CATGTTGAAGGTGACGACGATCTC-3´
18S rRNA forward: 5-TCCACCACCACAGAGAGAGG-3´
18S rRNA reverse: 5-GACAGTGCTCCTCAGATAAA -3´

Primers for Si transporter genes were designed from a highly conserved region of *ZmLsi1* and *ZmLsi2*, (NCBI accession No. of DQ524811.1 and AB495341.1, respectively). Primers of *ZmLsi6* were designed based on *OsLsi6* (AB253627.1). *ZmLsi6* was registered for the first time for maize in NCBI with the accession No. of KT003707.

Cycling conditions were as follows: Initial denaturation at 95 °C for 2 minutes followed by a definite number of cycles (according to the cycles being set up for each gene) of 94 ℃ for 45s, 60-61 ℃ (depending on the primers being used) for 45s, 72 ℃ for 45s, and a final extension of 72 ℃ for 5 min. PCR products were separated on 1% agarose gel electrophoresis. The band intensity on the gel stained with ethidium bromide was measured by UV Documentation Luminescent Image Analysis software (England) and then quantified by Image GFauge software. The results were expressed as the ratio of the intensity of the interested genes band to that of 18S rRNA to account for any differences in the starting amounts of RNA. The nucleotide sequences of amplified fragments were confirmed by DNA sequencing bidirectional using specific primers (Macrogen, Korea).

Statistical Analysis

The experiment was structured following a Completely Randomized Design (CRD) with three replications. Data from quantitative parameters were analyzed using ANOVA (SAS Version 8.1), and means were compared by Duncan's Multiple Range Test (DMRT).

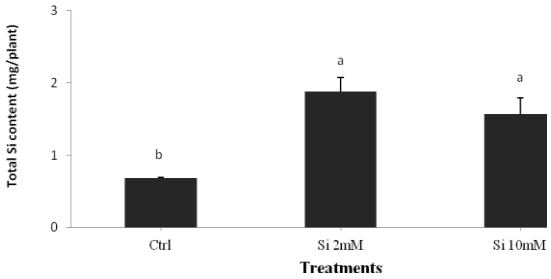

Fig. I. Total Si contents measured in whole maize seedlings under three Si treatments; data are presented as the means ± SD with n = 3. Different letters indicate significant differences by DMRT (*P*≤ 0.05).

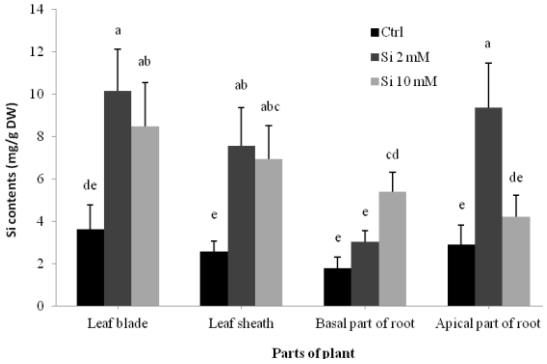

Fig. II. Silicon contents measured in different parts of maize seedlings under three Si treatments; data are presented as the means ± SD with n = 3. Different letters indicate significant differences by DMRT (*P*≤ 0.05).

Results

Si content of different parts of plant

Treatment of maize seedlings with 2 and 10 mM Si significantly increased their total Si content (1.88 and 1.56 mg/plant, respectively, compared to the control group 0.68 mg/plant). No significant difference however was observed between total Si content of 2 and 10 mM treated seedlings (Fig. I). Allocation of Si among different parts of control maize seedling was almost similar. In 2 mM Si treatment however, the Si content of basal parts of roots was significantly lower than other parts of the seedling. In 10 mM Si treatments, an increasing tendency was observed from apical part of the root (4.2 mg g^{-1}DW) toward the leaf sheath (6.9 mg g^{-1}DW) and leaf blade (8.4 mg g^{-1}DW) (Fig. II).

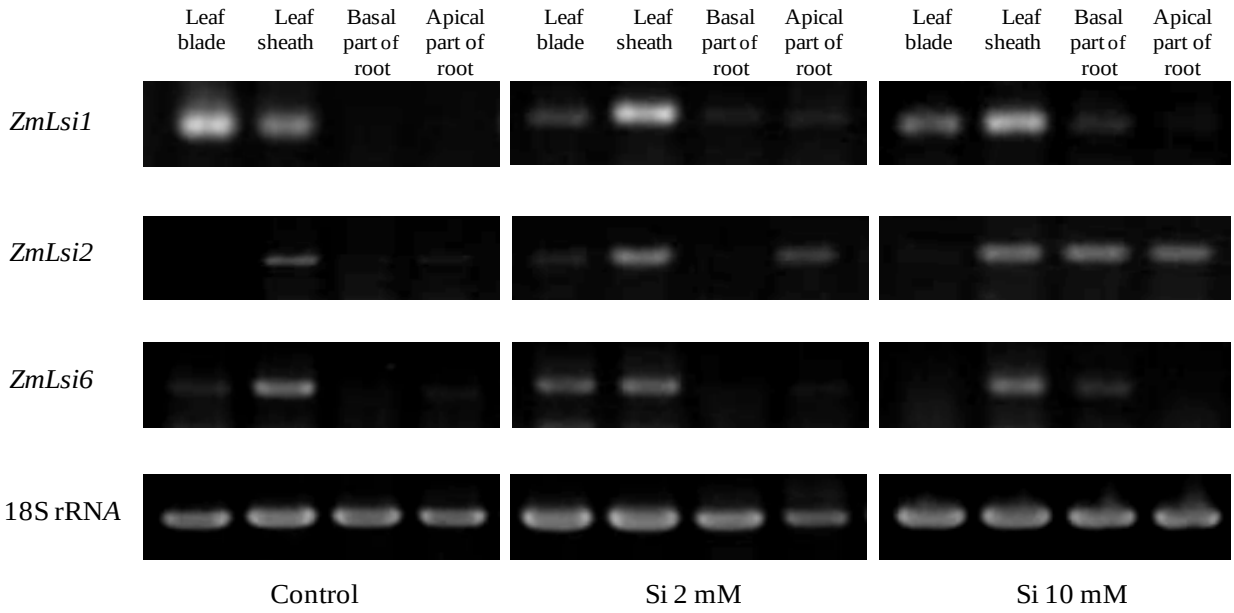

Fig. III. Semi-quantitative RT-PCR analysis of the expression of the Si transporters in different parts of maize seedling under control, 2 mM, and 10 mM Si treatments in comparison with the 18S rRNA, and quantification of the expression level using UV tech software.

Expression of Si transporter genes

Relative expression of *ZmLsi1* was significantly higher in leaf sheaths and blades than the roots in both the control and Si-treated seedlings while it was identical in aerial parts of seedlings of all treatments. Effect of 10 mM Si supply on the expression of *ZmLsi1* was higher than 2 mM and was more pronounced in roots (Figs. III & IV).

Treatment with Si, particularly of 10 mM, increased the expression of *ZmLsi2* in leaf sheaths and roots of maize seedlings, compared with the control group (Figs. III & V). The highest expression of *ZmLsi2* was detected in leaf sheaths followed by apical parts of roots of 2 mM Si treatment (Figs. III & V). In 10 mM Si treatment, leaf blades had the lowest expression of *ZmLsi2*, but in the other parts of maize seedlings the expression was identical. Application of both 2 and 10 mM Si significantly increased the relative expression of *ZmLsi2* in leaf sheaths and apical parts of roots, compared to the control group. Moreover, the expression of *ZmLsi2* in 10 mM Si treatment significantly decreased in leaf sheaths while it increased in roots, compared with 2 mM Si supply (Figs. III & V).

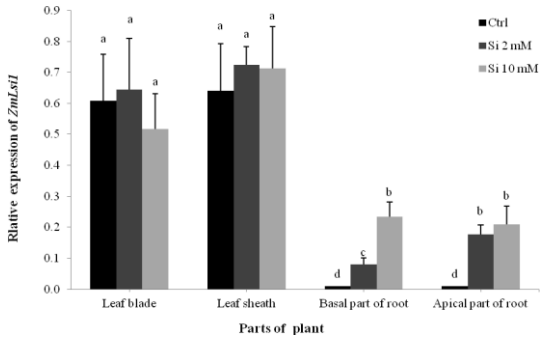

Fig. IV. Relative expression of *ZmLsi1* in different parts of maize seedlings under control, 2 mM and 10 mM Si treatments in comparison with the 18S rRNA; data are presented as the means ± SD with n = 3. Different letters indicate significant differences by DMRT ($P \leq 0.05$).

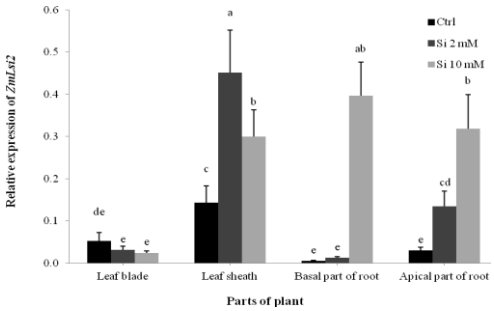

Fig. V. Relative expression of *ZmLsi2* in different parts of maize seedlings under control, 2 mM, and 10 mM Si treatments in comparison with the 18S rRNA; data are presented as the means ± SD with n = 3. Different letters indicate significant differences by DMRT ($P \leq 0.05$).

Under control conditions, the highest expression of *ZmLsi6* was observed in leaf sheaths (Figs. III & VI). In the 2 mM Si treatment, the highest and the lowest rates of *ZmLsi6* expression was observed in leaf sheaths and roots, respectively. Similarly, in the 10 mM Si treatment seedlings also the highest rate of *ZmLsi6* expression was observed in leaf sheaths (Figs. III & VI). Application of 2 mM Si significantly increased the expression rate of *ZmLsi6* in leaf blades compared to the control group. The effect of 10 mM Si on the expression of ZmLsi6 was more pronounced, significantly increasing its expression in both leaf sheaths and basal parts of roots, compared with the control group (Figs. III & VI).

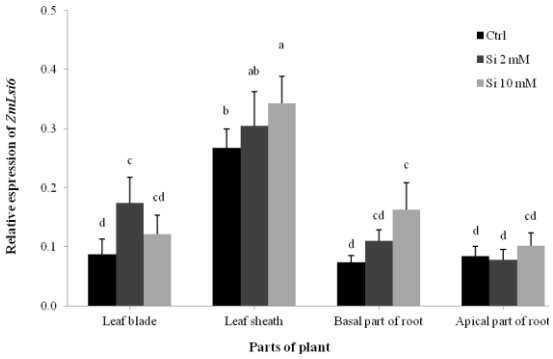

Fig. VI. Relative expression of *ZmLsi6* in different parts of maize seedlings under control, 2 mM, and 10 mM Si treatments in comparison with the 18S rRNA; data are presented as the means ± SD with n = 3. Different letters indicate significant differences by DMRT ($P \leq 0.05$).

Discussion

Si allocation

The study of Si content in the control group indicated that each part of maize seedling contained Si ranging from 0.2% to 0.4% of its dry weight. Because of the absence of Si in control seedlings nutrition solution, this amount of Si may be due to mineral storage of maize seeds. It is even possible that a part of Si in control plants came from water in nutrient solution because even highly purified water contains about 20 nM Si (Werner and Roth, 1983). Application of 2 mM Si remarkably increased Si content of maize seedlings (almost by twofold), which demonstrated Si absorption by seedlings. However, no significant increase in Si content of seedlings was observed when the concentration of external Si increased from 2 to 10 mM. This suggests that the capacity of Si absorption/translocation by maize seedlings is limited.

Early studies on Si uptake by rice suggested that Si is translocated to shoots by transpiration volume flow through the xylem. It has been reported that more than 90% of Si taken up by rice roots was translocated to the shoots (Ma and Takahashi, 2002). Wang et al., (2004) indicated that Si contents of the root segments of Si-treated maize plants gradually increased from the apical to the more basal root sections. Gao et al. (2006) reported that Si content of roots and shoots of maize plants increased from 0.2% and 0.6% of DW (in control group) to 0.6% and 2.2% DW in 2 mM Si-treated plants. These results indicate that Si is more abundant in shoots.

It was interesting to observe that treatment of maize seedlings with 2 mM Si in the present study resulted in accumulation of much part of Si in apical parts of roots, in addition to leaf blades. Moreover, in 10 mM Si-treated seedlings, a slight slope was observed in Si content from apical part of root toward the leaf blade. It demonstrates that the maize seedlings tend to translocate Si from roots to shoots under higher concentrations of exogenous Si. More recent research suggests that both active and passive Si-uptake components co-exist in maize with their relative contribution being dependent on external Si concentrations (Liang et al., 2006). In addition, an increase in Si concentration in the nutrition solution does not necessarily increases Si uptake by maize seedlings but changes the distribution pattern of Si in plants.

Distribution pattern of Si transporters

There are controversial reports on the spatial expression of Si transporters. Some previous studies have shown that *ZmLsi1* and *ZmLsi2* were mainly expressed in roots of barley and maize (Chiba et al., 2009; Mitani et al., 2009a). Mitani et al. (2009b) reported that the mRNA of *ZmLsi1* was mainly expressed in roots and there was no expression in the leaf sheaths and blades. Similarly, in rice *OsLsi1* was constitutively expressed in the roots, and within a root it was

mainly expressed in the basal region, with lower expression in the root tip regions (Yamaji and Ma, 2007). Unlike these reports, Mitani-Ueno et al., (2011) observed the expression of *Lsi2* homologs in both roots and shoots of pumpkin. Expression of *Lsi2* in the node of barley at the reproductive stage has been reported by Yamaji et al., (2012) as well. Some studies revealed that various cultivars of barley have different expression levels of *Lsi2* (Mitani et al., 2009b), suggesting that the expression of *Lsi2* is not only tissue specific but also species specific. In the present study, under normal conditions the relative expression of ZmLsi1 and ZmLsi2 were higher in shoots of maize seedlings than their roots.

Therefore, the used cultivar of maize (merit) in current study may have high level expression of *Lsi1* and *Lsi2* transporter in its shoots compared with other cultivars. It is also possible that high level of *ZmLsi1* expression in aerial parts of maize is related to the uptake of other nutrients such as boron. It has been suggested that the silicon uptake channel OsNIP2;1 (Lsi1) may mediate root boron uptake (Schnurbusch et al., 2010; Hanaoka et al., 2014).

There are some reports finding higher expression of *LSi6* gene in leaf sheathes but lower expression in roots of maize (Mitani et al., 2009b) and rice (Ma et al., 2011). Similarly, in the present study *ZmLsi6* was mainly expressed in leaf sheaths but had low relative expression in blade and roots of maize seedlings under control conditions. This implies the role of Lsi6 transporter in symplastic pathway delivery of Si to the growing leaf blade cells.

Exogenous supply of Si (particularly in 10 mM) remarkably induced the expression of *ZmLsi1* and *ZmLsi2* in roots of maize seedlings. *ZmLsi1* is located in epidermal, hypodermal, and cortical cells, and together with *ZmLsi2,* which is located in endodermis of maize roots, it is responsible for influx of Si from the external medium into the stele (Mitani et al., 2009a; Ma et al., 2011). There are three patterns in the effect of Si on the expression of Lsi1 genes in plants species. It may be downregulated (e.g., in rice), unaffected (e.g., in maize, barley, and wheat), or upregulated (e.g., in cucumber) by Si (Ma and Ymaji, 2015). In an orchestrated manner with *ZmLsi1* and *ZmLsi2*, expression of *ZmLsi6* was upregulated in leaf sheath in Si-supplied plants and resulted in higher Si contents of roots, leaf sheath, and leaf blades, compared with the control group. Similarly, Bokor et al. (2014) found that the addition of Si did not affect the expression level of *ZmLsi6* in the first leaf of maize plants but was upregulated in the second leaf.

Ma et al. (2007) showed that in rice, in contrast to Lsi1 which is localized in distal side, Lsi2 protein is localized on the proximal side of the plasma membrane in both the exodermis and the endodermis. Expression of *Lsi2* in Xenopus oocytes did not result in influx transport activity for silicon, but preloading of the oocytes with silicon resulted in a release of silicon, indicating that Lsi2 is a silicon efflux transporter. Identification of this silicon transporter revealed a unique mechanism of nutrient transport in plants: having an influx transporter on one side and an efflux transporter on the other side of the cell to permit the effective trans-cellular transport of the nutrients. Also noteworthy, the study suggests the rate of increase of Si uptake by maize seedlings was not proportional to the increase in its supply, and unexpectedly, the Si content of maize seedlings did not increase when the Si supply increased to 10. It was also interesting to find that among three examined Si transporters, the response of Lsi2 was discriminative to the external Si concentration so that under 10 mM Si, the expression of Lsi2 was noticeable. This suggests that Lsi2 may have a role in efflux of Si in maize under high concentrations of external Si. This hypothesis is currently under evaluation by a series of detailed experiments.

Conclusion

Results of the present study indicated that silicon content in aerial parts of maize seedlings was higher than the roots under 2 and 10 mM Si treatments. The results also showed that relative expression of *ZmLsi1* and *ZmLsi2* in shoots of maize seedlings grown under normal conditions was significantly higher than roots; however, *ZmLsi6* was mainly expressed in leaf sheaths. Application of Si significantly increased expression levels of all three silicon transporters. Among these transporters, the response of Lsi2 was

discriminative to the external Si concentration so that under 10 mM Si, the expression of Lsi2 was noticeable. This suggests that Lsi2 may have a role in efflux of Si in maize under high concentrations of external Si.

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