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Silicon decreases chloride transport in rice (*Oryza sativa* L.) in saline conditions

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ABSTRACT

Silicon can alleviate salt damage to plants, although the mechanism(s) still remains to be elucidated. In this paper, we report the effect of silicon on chloride transport in rice (*Oryza sativa* L.) seedlings in saline conditions. In the absence of salinity, silicon enhanced the growth of shoots, but not roots in three cultivars (cv. GR4, IR36, and CSR10). Salinity reduced the growth of both shoots and roots in all three genotypes. In saline conditions, addition of silicon to the culture solution again improved the growth of shoots, but not of roots. Under these saline conditions, the concentrations of chloride in the shoot were markedly decreased by adding silicon and the ratio of K^+/Cl^- was significantly increased, while the concentration of chloride in the roots was unchanged. The decrease in chloride concentration in the shoot was correlated with the decrease in transpirational bypass flow in rice, as shown by the transport of the apoplastic tracer trisodium-8-hydroxy-1,3,6-pyrenetrisulphonic acid (PTS). Addition of silicon increased the net photosynthetic rate, stomata conductance, and transpiration of salt-stressed plants in cv. IR36, indicating that the reduction of chloride (and sodium) uptake by silicon was not through a reduction in transpiration rate. Silicon addition also increased the instantaneous water use efficiency of salt-stressed plants, while it did not change the relative growth rate of shoots. The results suggest that silicon addition decreased transpirational bypass flow in the roots, and therefore decreased the transport of chloride to the shoot.

Introduction

Salinity stress is one of the main constraints that adversely affect crop yield and quality. About one-fifth of irrigated agricultural land is adversely affected by salinity (Chinnusamy et al., 2005). The problem of soil salinity is increasing because of the use of poor quality water for irrigation and poor drainage (Chinnusamy et al., 2005). Given the amount by which food production will have to be increased due to the growth of human population, it is desirable to increase the tolerance of crops to salinity stress. Plant nutritionists are trying to increase the tolerance to stress (including salinity) through the use of chemical additions to the soil.

Silicon is the second most abundant mineral element in the soil after oxygen (Epstein, 1999). In recent years, silicon transporters have been identified in several plants, such as rice, maize, barley and pumpkin (Ma, 2010; Mitani et al., 2011). Despite this, the roles of silicon in plant biology are still not fully understood (Epstein, 2009; Cooke and Leishman, 2011). Although it is deemed to be a non-essential nutrient for the majority of plants, silicon uptake has been found to be beneficial to plants and can improve the tolerance to a variety of biotic and abiotic stresses, such as pest and pathogen (Reynolds et al., 2009; Savvas et al., 2009), heavy metal stress (Neumann and Nieden, 2001; Nwugo and Huerta, 2008), drought (Hattori et al., 2005; Chen et al., 2011), and salt stress (Liang et al., 2003; Ashraf et al., 2010).

The roles of silicon in alleviating salt stress to plants have been observed in a good number of plant species, such as wheat (Ahmad et al., 1992; Saqib et al., 2008), maize (Liang et al., 2003), tomato (Al-aghabary et al., 2004), rice (Matoh et al., 1986; Yeo et al., 1999; Gong et al., 2006), cucumber (Zhu et al., 2004), canola (Hashemi et al., 2010), and sugarcane (Ashraf et al., 2010). However, the mechanisms by which silicon alleviates salinity stress are still not fully understood. In early years, it was suggested that silica deposition in the leaf decreased transpiration and therefore decreased salt accumulation (Matoh et al., 1986). Ahmad et al. (1992) proposed that silicon complexed sodium in the root and decreased sodium transport to the shoot, but direct evidence was not presented. More recently, much attention has been paid to silicon-mediated increases in antioxidant defense abilities of plants (Liang et al., 2003; Zhu et al., 2004; Soylemezoglu et al., 2009; Hashemi et al., 2010) and effects on ion transport.

The alleviative effect of silicon on salinity stress is related to decreased uptake of salt. Rice is a salt sensitive plant and salt damage to the seedlings occurs as a result of excessive transport of salt ions (generally sodium and chloride) to the leaves (Yeo et al., 1999).

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There has been extensive research into mechanism of sodium transport in plants (see review: Plett and Møller, 2010), and in rice, it has been demonstrated that the excessive sodium transport is largely the consequence of leakage along the apoplastic pathway (so called transpirational bypass flow) to the xylem (Garcia et al., 1997; Faiyue et al., 2010a, 2010b). Yeo et al. (1999) showed that the reduction of sodium uptake by added silicon in rice is accounted for by a reduction in transpirational bypass flow. Subsequently, more details of the effect of silicon on transpiration bypass flow and sodium concentration in the xylem sap was reported (Gong et al., 2006).

Chloride is an essential micronutrient and is involved in regulation of enzyme activities and many physiological processes (Flowers, 1988; Xu et al., 2000; White and Broadley, 2001). However, high concentrations of chloride can be toxic to plants. The critical chloride concentrations for toxicity in plants have been estimated to be 0.1–0.2 mmol g^{-1} dw (4–7 mg g^{-1} dw) and 0.4–1.4 mmol g^{-1} dw (15–50 mg g^{-1} dw) for sensitive and tolerant species, respectively (Xu et al., 2000). Although rice is relatively tolerant to chloride (Xu et al., 2000), yet high chloride concentrations can inhibit its growth. An (1992) observed that application of chloride (NH_4Cl plus $CaCl_2$) to loamy meadow soil at a rate of less than 400 mg kg^{-1} did not influence the growth and development of potted rice plants, while application of chloride of more than 600 mg kg^{-1} inhibited the growth and decreased the yield. When the application rate was up to 3200 mg kg^{-1}, no plants survived. Yin et al. (1990) found that irrigation with water containing 50–150 g Cl m^{-3} (about 1.4–4.2 mM) increased the dry mass of rice: with increasing chloride concentration, the dry mass decreased. Therefore, in saline conditions, high concentrations of chloride are another potential toxic ion besides sodium in rice. However, the transport of chloride in plants has received less attention and is less well understood in comparison to that of sodium (Teakle and Tyerman, 2010). Although silicon has been shown to decrease sodium transport in rice (Yeo et al., 1999; Gong et al., 2006), much less information is available about the effect of silicon on chloride accumulation in rice. In this paper, we report the effect of silicon on chloride transport in rice. The possible mechanism by which silicon mediates chloride accumulation is discussed.

Materials and methods

Plant material

Seeds of rice (*Oryza sativa* L.) were originally obtained from the International Rice Research Institute (IRRI, Los Baños, Laguna, Philippines) and multiplied in Sussex. Three cultivars were used in the present study: GR4, CSR10 and IR36, which were salt sensitive, salt tolerant and of intermediate tolerance, as shown in a previous study (Yeo et al., 1999). After being washed with deionized water, seeds were imbibed in aerated deionized water for 24 h and then sown on a floated nylon mesh in a 3-L black painted container filled with modified Yoshida culture solution as described in previous work (Yeo et al., 1999) in a growth cabinet (Conviron Model E15; Winnipeg, Canada; modified at the University of Sussex to include eight Osram Powerstar HQ1-BT lamps or a Weiss 2400E/+5 JU-Pa-S growth cabinet; Weiss Technik, Gmbh, Reiskirchen-Lindenstruth, Germany) or in a glasshouse within the School supplemented with high-pressure sodium lamps (GEC SON/T 400 w; Camplex Plant Care Thermoforce Ltd, Cockermouth, Cumbria, UK). The maximum temperature in the daytime and minimum temperature at night was 32 and 22 °C, respectively. The relative humidity was 40–70%. Seven-day-old seedlings were transplanted into 3-L black painted containers. In the growth cabinets, the photoperiod was 12 h with photosynthetically active radiation of between 250 and 400 μmol m^{-2} s^{-1}, the temperature ranged from 29 to 31 °C and the relative humidity from 30 to 40%. During the dark period (12 h), the temperature was 25–27 °C and the relative humidity was 30–45%.

NaCl and silicon treatments

Fourteen-day-old seedlings were treated with NaCl at a concentration of 50 mM. Silicate was applied when the seedlings were either 7 or 14 days old. The source of additional silicon was sodium silicate (BDH, Poole, Dorset, UK; 25.5–28.5% SiO_2) solution. Silicate was added to produce a final concentration of 3 mM, and the solution pH was adjusted to 4.5 – the same pH as that of the non-silicon treatment solution.

Transpirational bypass flow

Transpirational bypass flow was estimated using a fluorescent, membrane-impermeant dye, trisodium salt of 8-hydroxy-1,3,6-pyrenetrisulphonic acid (PTS) according to the method described by Yeo et al. (1999). The seedlings were transplanted into black-painted boxes at day 7 and silicon was added to the culture solution at the same time. At day 14, the plants were treated with 50 mM NaCl and 0.06 mM (30 mg/L) PTS. After 24 h, the shoots were collected for analysis.

Determination of ions and PTS fluorescence

Plant tissues were extracted in distilled water for 2 h at 90 °C, as described previously (Yeo et al., 1999). Chloride was determined with a chloride electrode (Cl801, VWR). Sodium and potassium in the extracts were measured by atomic absorption spectroscopy (Unicam 919). PTS fluorescence was measured at $\lambda_{excitation} = 403$ nm and $\lambda_{emission} = 510$ nm with a fluorescence spectrometer (Perkin-Elmer LS-3B).

Gas exchange

NaCl (50 mM) was applied to 14-day-old seedlings which had been raised in the growth chamber. At day 15, the plants were transferred to the glasshouse. Photosynthetic gas exchange parameters (P_N, g_s, E and C_i) were assayed at noon with a CIRAS-1 photosynthesis system (UK) on the most recent fully expanded leaves when the seedlings were 18 days old. At the time of measurement, the photosynthetic active radiation at the plant canopy was about 300 μmol m^{-2} s^{-1} and leaf temperature was 22–24 °C.

Statistical analysis

The data were generally subjected to statistical analysis by ANOVA using SPSS 15.0 for windows (SPSS, Chicago, IL, USA).

Results

Growth of rice seedlings under NaCl stress

In non-stress conditions, silicon enhanced the growth of shoots of all three rice cultivars in culture solution. As shown in Table 1, added silicon increased the plant height and shoot dry weight. Silicon addition had no effect on the root dry weight, although the root (seminal root) length was slightly decreased. Salt stress decreased the biomass of both shoot and root, and added silicon improved the growth of shoot, as shown by the plant height and shoot dry weight