Is the effect of silicon on rice uptake of arsenate (As^{V}) related to internal silicon concentrations, iron plaque and phosphate nutrition?

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Arsenate uptake by rice seedlings is affected by both Si (internal and external) and iron plaque on root surface.

Abstract

Solution culture experiments were conducted to investigate the effects of silicon (Si) on arsenate (As^{V}) uptake by rice. The addition of Si to the pretreatment or uptake solution significantly decreased shoot and root As concentrations ($P < 0.001$ and $P < 0.05$). The presence of Si in the pretreatment or uptake solution also significantly decreased shoot P concentrations ($P < 0.001$). The data demonstrated that both internal and external Si inhibited the uptake of As and P. Results of As uptake kinetics showed that the mechanism of the effect of Si on arsenate uptake is not caused by direct competition for active sites of transporters with As. The effect of Si on As uptake was not entirely mediated through the effect of Si on P uptake. Although the addition of Si to pretreatment solutions still significantly decreased shoot and root As concentrations, the extent of reduction became smaller when rice roots were coated with iron plaque.

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1. Introduction

Arsenic (As) is a widespread environmental contaminant posing serious health risks to humans and animals, and As-contaminated soils, sediments and water bodies are major sources of As contamination in food chains. Groundwater contamination with As is reported from many regions of the world with the most severe problems occurring in South-East Asia, such as Bangladesh, India and China (Wang and Jiang, 1994; Chen et al., 1995; Mandal et al., 1997; Nickson et al.,

1998; Chowdhury et al., 1999). Contaminated groundwater is not only used for drinking water but also extensively used for irrigation. Long-term use of As-contaminated groundwater for irrigation has resulted in elevated soil As levels in agricultural soils (Ullah, 1998; Alam and Satter, 2000). Paddy rice is the staple food crop in South-East Asia and As concentration as high as 1.8 mg kg^{-1} has been recorded in rice grain produced in the As-affected areas in Bangladesh (Meharg and Rahman, 2003). A recent risk analysis suggests that consumption of rice with elevated arsenic may cause health problems (Williams et al., 2005). Unfortunately, there are currently no effective countermeasures to reduce the risks associated with soil As contamination.

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Although silicon (Si) has not been listed among the essential elements for higher plants, it is well known that Si is beneficial for healthy growth and development of many plant species, especially graminaceous plants such as rice (*Oryza sativa* L.) (Lian, 1976; Liang et al., 1994; Epstein, 1994, 1999). Si is also well known to be effective in alleviating abiotic stresses in higher plants (Hodson and Evans, 1995; Rogalla and Römhild, 2002; Liang et al., 2003, 2005). Our previous study demonstrated that addition of Si to the nutrient solution can decrease As uptake by rice seedlings (Guo et al., 2005). The mechanisms involved in the effect of Si on uptake of As are so far not clear. It has been reported that effects of Si on P uptake are somehow dependent on the external P concentrations in the nutrient solution, and are also influenced by the Si already present in the plants (Ma and Takahashi, 1989, 1990). Arsenic and phosphorus are both Group V_A elements, and have similar electron configurations and chemical properties (Asher and Reay, 1979; Meharg and Macnair, 1992), but it is not clear if changes in internal Si and P concentrations in uptake solution can also affect arsenate uptake by rice.

An additional complication with rice is that, in the field, roots are usually coated with iron plaque due to the release of oxygen or oxidants into the rhizosphere, which promotes the oxidation of ferrous to ferric iron, the latter being precipitated on the root surface (Bacha and Hossner, 1977; Chen et al., 1980; Liu et al., 2004, 2005). It has been shown that the presence of iron plaque interferes with the conventional P–As interactions in soil–plant systems (Chen et al., 2005). We therefore hypothesize that the presence of iron plaque may also interfere with Si–As interactions.

Application of Si- and P-fertilizers is a common practice in rice production systems in Southeast Asia, so for the purpose of developing countermeasures to reduce As transfer to rice plants, it seems essential to understand the interactions between Si, P and iron plaque with regard to As uptake by rice plants. Therefore, the objectives of the present study were to investigate: 1) the effect of Si pretreatments on As uptake by rice seedlings; 2) the effects of Si and the pretreatment of rice with Si on the kinetics of As uptake by rice roots; 3) the interactive effect of Si and P on As; and 4) the effect of iron plaque on the interaction between Si and As.

2. Materials and methods

2.1. Experiment I: effect of Si pretreatments on arsenic uptake

Seeds of rice (*Oryza sativa* L. cv. Weiyou 77) obtained from the Agricultural Department of Hunan province were sterilized in 10% (v/v) H₂O₂ for 10 min followed by thoroughly washing in deionized water, and then germinated on moist perlite. After three weeks the seedlings were removed from the perlite and washed carefully under tap water to remove any adhering particles. Uniform seedlings were selected and transplanted in PVC pots (7.5 cm diameter × 14 cm high, one seedlings per pot) containing 500 ml modified Hoagland's nutrient solution containing (in mM): NH₄NO₃, 1.68; K₂SO₄, 0.67; MgSO₄, 0.50; CaCl₂, 1.33; KH₂PO₄, 0.44; and (in μM), Fe (II)-EDTA, 25; CuSO₄, 0.5; ZnSO₄, 0.5; MnSO₄, 2.5; H₃BO₃, 5; Na₂MoO₄, 0.25; CoSO₄, 0.1; NaCl, 50. In addition to a control with no added Si, Si was added as K₂SiO₃ · nH₂O to the growth medium to yield final concentrations of 0.5 and 2 mM Si. These solutions were referred to as pretreatment solutions. After

two weeks, rice seedlings were exposed to arsenic (Na₃AsO₄ · 12H₂O, 13.3 μM As) with the same three silicon levels. Thus, treatments were in the following combination of pretreatment and Si concentration in uptake solution: 0 (pretreatment) to 0, 0.5 or 2 mM Si (uptake solution); 0.5 to 0 or 0.5 mM Si; and 2 to 0 or 2 mM Si, giving seven treatments all together. Potassium (as 0.4 M KCl solution) was added differentially to give all treatments the same K concentration introduced by potassium metasilicate in the medium. The rice seedlings were grown in a controlled environment greenhouse with ambient light (roughly 13 h day/11 h night, 500–1100 μmol m⁻² s⁻¹). Temperature fluctuation in the greenhouse was between 20 and 35 °C at day and night. The relative humidity was 70%. Nutrient solutions were renewed twice a week, and the pH was adjusted to 5.5 using 0.1 M KOH or HCl. There were three replicates in a fully randomized design and the pots were re-randomized every day during the growth period. The rice seedlings were harvested after three more weeks.

2.2. Experiment II: effects of Si treatments on kinetics of Arsenate uptake by rice roots

The cultivation method of rice seedlings was the same as described above. After growing three weeks in perlite, uniform seedlings were selected and transplanted to PVC pots (one seedling each pot) containing 500 ml modified Hoagland's nutrient solution. The seedlings were allowed to grow in a growth chamber with 14/10 h light/dark cycle. The light intensity was 280 μmol m⁻² s⁻¹. Three weeks after transplanting, rice seedlings were grown with or without silicon (K₂SiO₃ · nH₂O, 1 mM Si) in the same nutrition solution as the pretreatment. Potassium (as 2 M KCl solution) was added to give all treatments the same K concentration. After a further two weeks, roots were excised at the basal node and used to measure kinetics of As uptake. Care was taken to ensure the roots were exposed to air for a minimal period.

Roots were excised and incubated in deionized water for 20 min at room temperature and were then transferred to conical flasks containing 1000 ml test solution, and incubated for further 30 min according to Meharg and Jardine (2003) and Chen et al. (2005). The test solutions with different concentrations of As were 1.5, 3.0, 7.5, 15.0, 30.0 and 75.0 μM. The test solution contained an additional 1 mM Si (K₂SiO₃ · nH₂O) or no Si. A stock solution of As was prepared from sodium arsenate (Na₃AsO₄ · 12H₂O). All test solutions contained 5.0 mM 2-(N-morpholin) ethansulfonic acid (MES) and 0.5 mM Ca(NO₃)₂ with the pH adjusted to 6.5 using KOH or HCl. Finally, the roots were thoroughly rinsed with an ice-cold solution containing 1 mM K₂HPO₄, 5 mM MES and 0.5 mM Ca(NO₃)₂ for 20 min to remove the As species in the free space of the roots. The roots were oven-dried at 70 °C for 72 h, weighed, and analyzed.

2.3. Experiment III: effect of silicon on As uptake with different P concentrations in the nutrient solution

Seedlings (three weeks old) prepared as described above were transferred to PVC pots (one seedling per pot) containing 500 ml modified Hoagland's nutrient solution (pH 5.5). After 20 days, rice seedlings were exposed to 13.3 μM As as Na₃AsO₄ · 12H₂O with two levels of Si (0, 1 mM Si, as K₂SiO₃ · nH₂O) and 4 levels of P (6.5, 13, 130 and 260 μM). Potassium (as 2 M KCl solution) was added differentially to give all treatments the same K concentration in the medium. The seedlings were grown in a growth chamber with 14/10 h light/dark cycle. The light intensity was 280 μmol m⁻² s⁻¹. The rice seedlings were harvested after further 18 days. The As and P concentrations in shoots and roots were determined as described in Section 2.5.

2.4. Experiment IV: a short-term As uptake (up to 24 h) by rice roots with or without iron plaque

Seedlings (three weeks old) prepared as described above were transferred to PVC pots (one seedling per pot) containing 500 ml modified Hoagland nutrient solution (pH 5.5). The solution culture experiment was performed in four stages. At stage I, all seedlings were grown in normal nutrient solution (–Si) for 20 days. At stage II, half of the seedlings were transferred to nutrient

solution containing 1 mM Si as $K_2SiO_3 \cdot nH_2O$ (+Si). This stage lasted for 12 days. At stage III, –Si and +Si seedlings were each divided into two groups and iron plaque were induced on the roots as follows (–Si – Fe, –Si + Fe, +Si – Fe, +Si + Fe). Prior to iron plaque induction, all seedlings were placed in deionized water for 6 h to minimize interference from other elements with iron. They were then transferred to 500 ml solution with 1.43 mM of ferrous ion for 24 h (Fe^{2+} as $FeSO_4 \cdot 7H_2O$). Solution pH was adjusted to 5.5 using 0.1 M KOH or HCl. All seedlings were subsequently grown in nutrient solution for 6 h, before exposure to As. At stage IV, all seedlings were exposed for 24 h to nutrient solution containing 13.3 μM As ($Na_3AsO_4 \cdot 12H_2O$) with (1 mM, $K_2SiO_3 \cdot nH_2O$) or without Si. Thus, there were eight treatments for the experiment (–Si – Fe – Si, –Si – Fe + Si, –Si + Fe – Si, –Si + Fe + Si, +Si – Fe – Si, +Si – Fe + Si, +Si + Fe – Si, +Si + Fe + Si). Each treatment was replicated four times, giving a total of 32 pots.

2.5. DCB extraction of iron plaque from roots and chemical analysis of Plant tissues

At harvest, iron plaque on fresh root surfaces was extracted using dithionite-citrate-bicarbonate (DCB) using the method of Taylor and Crowder (1983) and Otte et al. (1991). The whole root system of each seedling was incubated for 30 min at room temperature (20–25 °C) in 30 ml of solution containing 0.03 M sodium citrate ($Na_3C_6H_5O_7 \cdot 2H_2O$) and 0.125 M sodium bicarbonate ($NaHCO_3$), with the addition of 0.5 g sodium dithionite ($Na_2S_2O_4$). Roots were rinsed three times with deionized water that was added to the DCB-extracts. The resulting solution was made up to 50 ml with deionized water. After DCB extraction, roots and shoots were oven-dried at 70 °C for 72 h and weighted.

At harvest, plants were divided into roots and shoots, and oven dried at 70 °C for 72 h and the dry weights of shoots and roots were determined. Dried shoots and roots were finely ground in a stainless steel mill. Subsamples were then placed in 100 ml Teflon tubes and digested by 5 ml of high-purity nitric acid using the CEM Microwave Sample Preparation System (Matthews, NC, USA). The temperature was raised to 180 °C within 15 min and held for 15 min. After digestion, the solutions were cooled, diluted to 50 ml with ultra-pure water (Easy-pure) and filtered into acid-washed plastic bottles. The concentrations As and P in the DCB-extract and acid digest solution were determined by ICP-OES (Inductively Coupled Plasma-Optical Emission Spectrometer, Optima 2000 DV, Perkin Elmer, USA) and atomic fluorescence spectrometry (A2022; Beijing Haiguang Analytical Instrument Co., Beijing, China), respectively. A reagent blank and standard reference sample (tea leaves obtained from the National Research Center for Standards, China) were used to ensure the accuracy and precision of digestion and subsequence analysis.

2.6. Data analysis

Analysis of variance (ANOVA) on plant biomass and concentrations of As and P was performed using Windows-based Genstat (6th edition, VSN Ltd, England).

3. Results

3.1. Plant biomass (Experiment I)

Compared with the –Si – Si treatment (control), pretreatment with Si (+Si – Si) had little effect on plant biomass (Table 1). The addition of Si to the As uptake solution significantly increased shoot dry weights (Table 1, $P < 0.05$), but had no significant effect on root dry weights.

Table 1

Biomass ($g\ pot^{-1}$, dry matter basis) of rice seedlings grown in nutrient solution with one of three Si concentrations and one of four Si treatments (mean $\pm$ SE; $n = 3$)

Si Treatment	Si Level (mM)	Shoot dry weight (g)	Root dry weight (g)
–Si – Si	0.0	2.09 $\pm$ 0.25	0.69 $\pm$ 0.09
+Si – Si	0.5	2.37 $\pm$ 0.16	0.83 $\pm$ 0.04
–Si + Si	0.5	2.72 $\pm$ 0.09	0.81 $\pm$ 0.05
+Si + Si	0.5	2.54 $\pm$ 0.15	0.77 $\pm$ 0.06
+Si – Si	2.0	1.82 $\pm$ 0.19	0.59 $\pm$ 0.04
–Si + Si	2.0	2.57 $\pm$ 0.23	0.70 $\pm$ 0.10
+Si + Si	2.0	2.60 $\pm$ 0.14	0.66 $\pm$ 0.05
Analysis of variance			
Si Treatment		$P < 0.05$	NS
Si Level		NS	$P < 0.05$
Si Treatment $\times$ Si Level		NS	NS

NS means not significant.

3.2. As and P in shoots and roots (Experiment I)

As shown in Table 2, the addition of Si to the pretreatment or uptake solution significantly decreased shoot ($P < 0.001$) and root ($P < 0.05$) As concentrations. There was a significant difference between treatments of Si levels in root As concentrations (Table 2, $P < 0.05$), but no difference in shoot As concentrations.

Similar to As, the addition of Si to the pretreatment or uptake solution significantly decreased shoot P concentrations (Table 2, $P < 0.001$). However, Si in the pretreatment or uptake solution significantly increased root P concentrations (Table 2, $P < 0.05$). There was a significant difference in shoot and root P concentrations between Si levels (Table 2, $P < 0.05$ and $P < 0.001$, respectively).

3.3. Effects of silicon on arsenate uptake kinetics (Experiment II)

In all treatments, As influx into rice roots followed a hyperbolic pattern, indicating that As influx increased with increasing concentrations of As in the incubation solutions (Table 3). As uptake kinetics was adequately described by the Michaelis-Menten function in all treatments. However, As influx was significantly different between different silicon treatments. Compared with the –Si – Si treatment, the K_m value for the –Si + Si treatment was hardly changed, but the V_{max} value was significantly decreased (Table 3, $P < 0.05$). No significant difference in the V_{max} and K_m values was observed either in +Si – Si or +Si + Si treatments (Table 3).

3.4. Effect of silicon on arsenate uptake with different external P concentrations (Experiment III)

When P concentrations were 6.5 and 13 μM , the addition of Si had no significant effect on shoot P concentrations (Fig. 1a). However, Si significantly decreased shoot P concentrations when P concentrations in nutrient solution were 130 and 260 μM (Fig. 1a, $P < 0.001$). The addition of Si had no

Table 2

Mean As and P concentrations in shoots and roots of rice grown in nutrient solution containing 13.3 μM As with one of three Si concentrations and one of four Si treatments

Si Treatment	Si Level (mM)	Shoot		Root	
		As conc. (mg kg^{-1})	P conc. (mg kg^{-1})	As conc. (mg kg^{-1})	P conc. (mg kg^{-1})
–Si – Si	0.0	34.43 $\pm$ 4.40	9394 $\pm$ 218.5	1037 $\pm$ 81.69	3572 $\pm$ 138.9
+Si – Si	0.5	21.55 $\pm$ 3.61	7864 $\pm$ 288.3	806.7 $\pm$ 85.59	3625 $\pm$ 346.0
–Si + Si	0.5	19.42 $\pm$ 1.43	6904 $\pm$ 95.38	915.1 $\pm$ 24.93	3909 $\pm$ 56.35
+Si + Si	0.5	19.44 $\pm$ 0.75	7027 $\pm$ 102.7	901.2 $\pm$ 44.73	3344 $\pm$ 103.0
+Si – Si	2.0	22.51 $\pm$ 1.09	8358 $\pm$ 525.4	853.4 $\pm$ 32.58	4027 $\pm$ 169.7
–Si + Si	2.0	14.92 $\pm$ 1.36	5598 $\pm$ 110.1	672.7 $\pm$ 26.38	4683 $\pm$ 144.8
+Si + Si	2.0	15.33 $\pm$ 1.69	5625 $\pm$ 98.97	679.3 $\pm$ 21.95	4589 $\pm$ 102.0
Analysis of variance					
Si Treatment		$P < 0.001$	$P < 0.001$	$P < 0.05$	$P < 0.05$
Si Level		NS	$P < 0.05$	$P < 0.05$	$P < 0.001$
Si Treatment $\times$ Si Level		NS	$P < 0.05$	$P < 0.05$	$P < 0.05$

Error bars: standard errors ($n = 3$). NS means not significant.

significant effect on root P concentrations irrespective of external P concentrations (Fig. 1b). Addition of Si to nutrient solution significantly decreased both shoot and root As concentrations regardless of external P concentrations (Fig. 2a,b, $P < 0.001$).

3.5. Effect of silicon on arsenate uptake by rice roots with or without iron plaque (Experiment IV)

After 24 h of pretreatment with Fe^{2+} in solution, rice roots appeared reddish, indicating the formation of iron plaque; roots in –Fe treatments remained white. The presence of iron plaque was further indicated by Fe concentrations in dithionite-citrate-bicarbonate (DCB) extracts (Table 4). The addition of Si to the pretreatment solution had little effect on the formation of iron plaque on rice roots (Table 4). In general, irrespective of Si treatments, the presence of iron plaque lowered As concentrations in shoots and roots (Fig. 3). The addition of Si to pretreatment or uptake solutions significantly decreased both shoot and root As concentrations in rice plants without iron plaque on their root surface (Fig. 3a,b, $P < 0.05$). However, in the presence of iron plaque, the addition of Si to pretreatment solution significantly decreased shoot and root As concentrations (Fig. 3a,b, $P < 0.05$), while the addition of Si to uptake solution had little effect (Fig. 3a,b).

4. Discussion

The addition of Si to uptake solution containing As (–Si + Si) significantly increased shoot dry weights compared

Table 3

Parameters of kinetics for arsenate influx into rice (*Oryza sativa* L.) roots with four Si treatments

Treatment	$V_{\text{max}}^{\dagger}$ ($\text{nmol g}^{-1} \text{ d.wt min}^{-1}$)	$K_m^{\dagger}$ (mM)	R^2
–Si – Si	40.1 $\pm$ 6.2*	0.0243 $\pm$ 0.0089	0.950
+Si – Si	33.1 $\pm$ 2.3	0.022 $\pm$ 0.0037	0.989
–Si + Si	22.5 $\pm$ 3.7*	0.0186 $\pm$ 0.0079	0.935
+Si + Si	30.5 $\pm$ 2.9	0.0199 $\pm$ 0.0048	0.978

*Significant at $P = 0.002$.

Fig. 1. Mean P concentrations in shoots (a); and roots (b) of rice grown in nutrient solution containing 13.3 μM As with one of two Si concentrations and one of four P concentrations. Error bars: standard errors ($n = 4$).

Fig. 2. Mean As concentrations in shoots (a); and roots (b) of rice grown in nutrient solution containing 13.3 μM As with one of two Si concentrations and one of four P concentrations. Error bars: standard errors ($n = 4$).

to the -Si - Si treatment. This result is in agreement with our previous report (Guo et al., 2005). Si pretreatment with no As exposure (+Si - Si) had no beneficial effect on shoot dry weights compared to the -Si - Si treatment. This result suggests that Si may play a beneficial role in alleviating As

Table 4

Iron (Fe) and arsenic (As) concentrations in dithionite-citrate-bicarbonate (DCB) extracts of roots surface of rice seedlings with or without Si, Fe²⁺ in pretreatment solution and Si in arsenic uptake solution

Treatment	DCB-Fe (mg g ⁻¹ RDW)	DCB-As (mg kg ⁻¹ RDW)
-Si - Fe - Si + As	1.71 ± 0.28	ND
-Si - Fe + Si + As	1.61 ± 0.25	ND
-Si + Fe - Si + As	21.35 ± 3.14	184.8 ± 21.48
-Si + Fe + Si + As	18.47 ± 1.18	165.6 ± 9.82
+Si - Fe - Si + As	1.06 ± 0.16	ND
+Si - Fe + Si + As	0.76 ± 0.09	ND
+Si + Fe - Si + As	18.69 ± 1.72	169.4 ± 15.97
+Si + Fe + Si + As	18.30 ± 0.99	165.0 ± 6.80

Data are means ± SE. ND, Not detectable. RDW, root dry weight.

Fig. 3. Mean As concentrations in shoots (a); and roots (b) of rice with or without iron plaque grown in nutrient solution containing 13.3 μM As with one of two Si concentrations and one of four Si treatments. Error bars: standard errors ($n = 4$).

toxicity. Positive effects of Si on plant growth under biotic and abiotic stresses have been reported elsewhere by Epstein (1994, 1999), and it is also well known that Si may improve plant growth at the late growth stage, since about 66% of silicon in the whole plant has been showed to be absorbed during the reproductive stage (Ma et al., 1989).

The addition of Si to the pretreatment or uptake solution significantly decreased shoot and root As concentrations, suggesting that both external and internal Si could affect As uptake. The kinetics study showed that in the treatment without Si the uptake kinetics were similar to those obtained by Meharg and Jardine (2003) and Chen et al. (2005). Uptake of As by rice roots was significantly influenced by -Si + Si treatment (Table 3). The addition of 1 mM Si to the uptake solution did not change the K_m value as compared to the treatment with no Si, but the V_{max} was decreased by nearly 50% (Table 3), indicating that the effect of Si on As uptake was

not mediated by a direct competitive effect of Si on active sites of As (P) transporter on root cell membranes.

Since in many plant species As is taken up via the Pi transport systems (Asher and Reay, 1979; Meharg and Macnair, 1992), the alternative reason for Si-mediated reduction in As uptake could be through its inhibitory effect on P uptake. Thus, factors affecting P uptake might also affect As uptake. From the results of Experiment I, this hypothesis is possible because the addition of Si to pretreatment and uptake solutions produced a similar degree of reduction in shoot As and P concentrations (Table 2). When the external P concentration in the medium was low ($<14 \mu\text{M}$), the inhibitory effect of Si on P uptake was hardly observed, but when the external P concentration was higher, the inhibitory effect became more pronounced. However, results from Experiment III showed that even at external P concentrations below $14 \mu\text{M}$, the addition of Si still significantly decreased shoot and root As concentrations (Fig. 2a,b, $P < 0.001$), but had little effect on shoot P concentrations (Fig. 1a, $P < 0.001$). Therefore, the effect of Si on As uptake could not be entirely explained by the effect on P uptake. A separate study using low Si rice mutant is being carried out to further investigate the mechanisms involved in Si-mediated reduction in As uptake by rice plants.

Due to the ubiquity of iron plaque on rice roots and the potential As sequestration in iron plaque, one should not neglect the confounding factor of iron plaque on root surface in interpreting the effect of Si on As uptake by rice plants observed in solution culture studies. The confounding effect of iron plaque should be considered when developing practical approach to reducing As accumulation by applying Si fertilizers. Results from the present study showed that the addition of Si to the pretreatment solution did not affect the formation of iron plaque on root surfaces (Table 4). However, the presence of iron plaque to some extent reduced the inhibitory effect of Si on As uptake (Fig. 3a,b). The fact that the presence of iron plaque reduced the effect of Si on As uptake might be due to the strong affinity of iron plaque for As. Strong sequestration of As in iron plaque may be a predominant process controlling As uptake by rice roots. However, these results should be viewed with care, since the amounts of iron plaque formed on root surface of rice plants grown in soil varied between root sections (Conlin and Crowder, 1989; Liu et al., 2005), and also between different growth stages even on the same root. Furthermore, Si application may promote the oxidation power of rice roots, which may lead to more deposition of iron oxides on the root surface under field conditions (Okuda and Takahashi, 1962; Cheng, 1982).

In conclusion, our results demonstrated that both external and internal Si affect As uptake by rice plants. The inhibitory effect of Si on As uptake is not mediated by direct competition between As and Si for uptake sites on root cell membranes. Despite the chemical similarity between As and P, the mechanisms of the inhibitory effect of Si on As uptake are probably different from that on P uptake. The presence of iron plaque altered the effect of Si on As uptake. Results from this study are important for the development of Si fertilizers to reduce As accumulation in rice grown in As-impacted soils.

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