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Effect of silicate on the growth and arsenate uptake by rice (*Oryza sativa* L.) seedlings in solution culture

W. Guo[1,2], Y.-L. Hou[2], S.-G. Wang[3] & Y.-G. Zhu[1,4]
[1]*Research Center for Eco-Environmental Sciences, The Chinese Academy of Sciences, Beijing 100085, P. R. China.* [2]*Graduate School of the Chinese Academy of Sciences, Beijing 100039, P. R. China.* [3]*Beijing University of Chemical Technology, Beijing 100029, P. R. China.* [4]*Corresponding author**

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Abstract

A solution culture experiment was conducted to investigate the effect of silicate on the yield and arsenate uptake by rice. Rice seedlings (*Oryza sativa* L. cv. Weiyou 77) were cultured in modified Hoagland nutrient solution containing three arsenate levels (0, 0.5 and 1.0 mg L^{-1} As) and four silicate levels (0, 14, 28 and 56 mg L^{-1} Si). Addition of Si significantly increased shoot dry weight ($P = 0.001$) but had little effect on root dry weight ($P = 0.43$). Addition of As had no significant effect on shoot dry weight ($P = 0.43$) but significantly increased root dry weight ($P = 0.01$). Silicon concentrations in shoots and roots increased proportionally to increasing amounts of externally supplied Si ($P < 0.001$). The presence of As in the nutrient solution had little effect on shoot Si concentration ($P = 0.16$) but significantly decreased root Si concentration ($P = 0.005$). Increasing external Si concentration significantly decreased shoot and root As concentrations and total As uptake by rice seedlings ($P < 0.001$). In addition, Si significantly decreased shoot P concentration and shoot P uptake ($P < 0.001$). The data clearly demonstrate a beneficial effect of Si on the growth of rice seedlings. Addition of Si to the growth medium also inhibited the uptake of arsenate and phosphate by the rice seedlings.

Abbreviation: ICP-OES – inductively coupled plasma-optical emission spectrometer

Introduction

The toxicity of arsenic (As) to humans is of widespread interest because of extensive areas of As contamination in southeast Asian countries such as Bangladesh and China (Dhar et al., 1997; Wang et al., 2002). Human exposure to As occurs primarily from food, water, and air. Excessive exposure can lead to a variety of adverse health effects such as skin conditions and respiratory, pulmonary, cardiovascular, and neurological problems (Mandal and Suzuki, 2002). There are natural and anthropogenic sources of As in the environment. Arsenic may accumulate in soil and water through the use of As-containing pesticides and fertilizers, atmospheric deposition from the burning of fossil fuels, disposal of industrial and animal wastes, and mining activities. The presence of elevated levels of As in soils or irrigation water may lead to elevated concentrations in rice grain or straw (Abedin et al., 2002). Recent studies indicate that the concentration of As in rice grain can reach 0.74 mg kg^{-1} in areas irrigated with contaminated groundwater (Abedin et al., 2002). Rice is one of the staple food crops in China. In the vicinity of an As mine in Hunan province up to

* FAX No: +86–10–62923563.
E-mail: ygzhu@mail.rcees. ac.cn

35% of the local population were reported to suffer from severe arsenism and the proportion affected increased with age (Wang et al., 1999). Epidemiological studies have demonstrated significant correlations between As levels found in human hairs and those in local rice, wheat and soils (Lin et al., 2001).

Silicon is the second most abundant element in soils, the mineral substrate for most of the world's plant life (Epstein, 1994). Rice is a typical siliciphilous plant and can accumulate concentrations of up to 10% Si in the shoots on a dry matter basis. Since Sommer (1926) demonstrated the favorable effect of Si on rice growth, intensive studies on the essentiality of Si for plants have been undertaken throughout the world. Although the essentiality of Si for plant growth has not yet been established (Epstein, 1994), there is sufficient evidence to suggest that it is an agronomically essential nutrient for achieving and maintaining high yields of rice (Lian, 1976; Liang et al., 1994). Silicon enhances the growth of various (mostly monocotyledonous) plants by providing rigidity to plant tissues and promoting photosynthesis (Cheng, 1982; Epstein, 1994). Furthermore, a protective role of Si against fungal infection, injuries inflicted by insects, and herbivory may also be involved (Adatia and Besford, 1986; Samuels et al., 1991).

There have been numerous reports that Si can affect P uptake by certain plant species. Okuda and Takahashi (1961a, b) showed that increasing Si decreased the concentration and uptake of P by rice plants in solution culture. Miyake and Takahashi (1978, 1983, 1985) also observed that the addition of silicic acid led to a significant reduction in P uptake by other plants such as tomato, cucumber, and soybean. Ma and Takahashi (1989, 1990) observed that the effect of Si on P uptake by rice plants was somehow dependent on the P supply level in the nutrition solution. These authors found that when the P concentration in the medium was low (0.014 m*M*), the retardation effect of silicic acid on P uptake was barely discernible, but with increasing levels of P in the medium the effect became more evident, especially at excessive levels. However, the explanations for the effect of Si on P uptake are various and can even be contradictory (Hall and Morison, 1906; Okuda and Takahashi, 1964; Smyth and Sanchez, 1980; Syouji, 1981). Arsenic and P are both Group V_A elements and thus have similar electron configurations and chemical properties. Arsenate also acts as a phosphate analogue with respect to transport across the root plasma membrane, with phosphate competing much more effectively for transport sites. In the relatively large number of plant species tested it has been shown that arsenate is taken up via the phosphate transport systems (Asher and Reay, 1979; Lee, 1982; Meharg and Macnair, 1992; Ullrich-Eberius et al., 1989). Until now, few investigations have been carried out on the effects of Si on As uptake and related mechanisms.

The objective of the present study was to investigate the effects of silicate on the growth of, and arsenate uptake by, rice seedlings in solution culture. It was hoped that the study would provide a basis for developing strategies for reducing the risks associated with As contamination in soils and maintaining sustainable rice production.

Materials and methods

Plant solution culture

Seeds of rice (*Oryza sativa* L. cv. Weiyou 77) obtained from the Agricultural Department of Hunan province were sterilized in 10% v/v H_2O_2 for 10 min followed by thorough washing in deionized water, and then germinated on moist perlite. After 20 days, the seedlings were removed from the perlite and washed carefully under tap water to remove any adhering particles. Seedlings of uniform size were selected and transplanted in PVC pots (7.5 cm diameter × 14 cm high, two seedlings pot^{-1}) containing 500 mL nutrient solution (modified Hoagland nutrient solution containing (in μM): NH_4NO_3, 1.68; K_2SO_4, 0.67; $MgSO_4$, 0.50; $CaCl_2$, 1.33; KH_2PO_4, 0.44; and (in μM), Fe(II)–EDTA, 25; $CuSO_4$, 0.5; ZnSO4, 0.5; $MnSO_4$, 2.5; H_3BO_3, 5; Na_2MoO_4, 0.25; $CoSO_4$, 0.1; NaCl, 50). After 15 days, $Na_3AsO_4 \cdot 12H_2O$ solution was added to the growth medium to final concentrations of 0, 0.5 and 1.0 mg L^{-1} As and $K_2SiO_3 \cdot nH_2O$ solution was added to final concentrations of 0, 14, 28 and 56 mg L^{-1} Si. Actual Si concentration was determined after making the solution, and respective volumes of the solution was added to the nutrient solution to achieve the final targeted Si concentration. Potassium (as 0.4 *M* KCl solution) was added differentially to give all treatments the same K concentration in the medium. The rice seedlings were harvested after a further 15 days. The seedlings grew in a growth chamber with 14/10 h light/dark cycle. The light intensity was about 280 μmol m^{-2} s^{-1}. The nutrient solution was renewed twice each week, and the pH was adjusted to 5.5 using 0.1 *M* KOH or HCl. There were four replicates in a fully randomized design and the pots were re-randomized every day during the growth period.

Plant analysis

At harvest, plants were divided into roots and shoots, oven dried at 70 °C for 48 h and the dry weights of shoots and roots were determined. Dried shoots and roots were finely ground in a stainless still mill. Subsamples were digested in 5 mL of high-purity nitric acid, first at 80 °C for 2 h, then at 120 °C for 30 h. After digestion, the solutions were cooled, diluted to 50 mL with ultra-pure water (Easy-pure) and filtered into acid-washed plastic bottles. As and P contents of the solution were determined by ICP-OES (inductively coupled plasma-optical emission spectrometer, VISTA-MPX, VARIAN, USA). A standard reference material (tea leaves obtained from China Standard Material Center) was used to ensure the accuracy and precision of digestion and analysis. The Si contents of shoots and roots were determined by the colorimetric molybdenum blue method described by van der Vorm (1987). Briefly, 300-mg samples of plant material were ashed in porcelain crucibles for 3 h at 550 °C, the ash was dissolved in 1.3% HF, then the Si concentrations in the solutions were measured by the colorimetric molybdenum blue method at 811 nm with a spectrophotometer.

Data analysis

Specific P or As uptake (SPU or SAsU) was calculated as the ratio of total P or total As uptake in each pot to the root dry weight in that pot. As or P translocation from roots to shoots (shoot As% or shoot P%) was calculated as the percentages of total shoot As or P uptake in shoots to total As or P uptake (root + shoot), respectively. All data were subjected to analysis of variance (ANOVA, SPSS).

Results

Plant yield

Shoot dry weights increased with increasing external Si concentrations in the culture solution (Table 1, $P = 0.001$). The highest shoot dry weight (1.32 g pot^{-1}, averaged over the three As treatments) occurred in solution to which 28 mg L^{-1} Si was added. Addition of Si to the culture solution at rates of 14, 28 and 56 mg L^{-1} resulted in increases in shoot dry weight of 24, 37 and 33%, respectively. The presence of Si in the culture solution had little effect on root dry weight in any treatment (Table 1, $P = 0.43$).

Increasing As concentration in the growth solution had no significant effect on shoot dry weight (Table 1, $P = 0.43$), but significantly increased root dry weight (Table 1, $P = 0.01$). The highest root dry weight (0.40 g pot^{-1}, averaged

Table 1. Biomass (g pot^{-1}, dry matter basis) of rice seedlings grown in nutrient solution with one of four Si levels and with one of three As levels (mean ± SE; $n = 4$)

As level (mg L^{-1})	Si level (m*M*)	Shoot dry weight (g)	Root dry weight (g)
0	0	1.02 ± 0.06	0.29 ± 0.01
	0.5	1.26 ± 0.11	0.34 ± 0.04
	1.0	1.25 ± 0.13	0.33 ± 0.03
	2.0	1.36 ± 0.23	0.33 ± 0.05
0.5	0	0.91 ± 0.09	0.35 ± 0.04
	0.5	1.04 ± 0.09	0.33 ± 0.04
	1.0	1.39 ± 0.03	0.42 ± 0.02
	2.0	1.20 ± 0.13	0.33 ± 0.05
1.0	0	0.97 ± 0.05	0.39 ± 0.02
	0.5	1.28 ± 0.07	0.43 ± 0.03
	1.0	1.33 ± 0.08	0.39 ± 0.03
	2.0	1.29 ± 0.08	0.37 ± 0.03
		Analysis of variance	
Si		$P = 0.001$	NS
As		NS	$P = 0.01$
Si × As		NS	NS

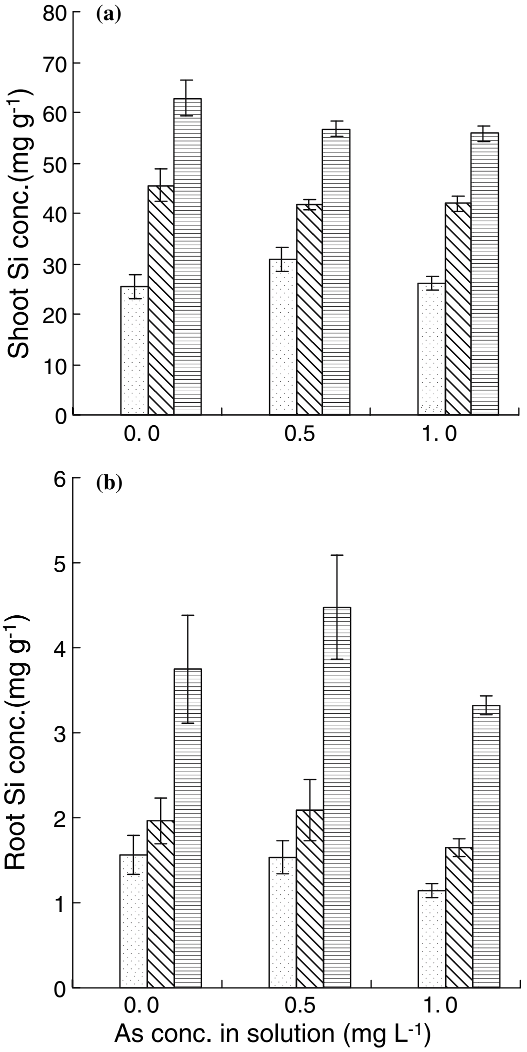

Figure 1. Mean Si concentrations in shoots (a) and roots (b) of rice plants grown in nutrient solution with one of three Si levels and with one of three As levels. ▢, 14 mg Si L^{-1}; ▧, 28 mg Si L^{-1}; and ▤, 56 mg Si L^{-1}. Error bars: standard errors ($n = 4$).

over the four Si treatments) was observed in the highest As treatment (1.0 mg L^{-1} As).

Shoot and root Si, As and P concentrations

Si concentrations in shoots and roots increased proportionally with increasing external Si concentration (Figure 1a, b, $P < 0.001$). The presence of As in the nutrient solution had little effect on shoot Si concentration (Figure 1a, $P = 0.16$). Addition of As at 0.5 mg L^{-1} did not affect root Si concentration, and addition of As at

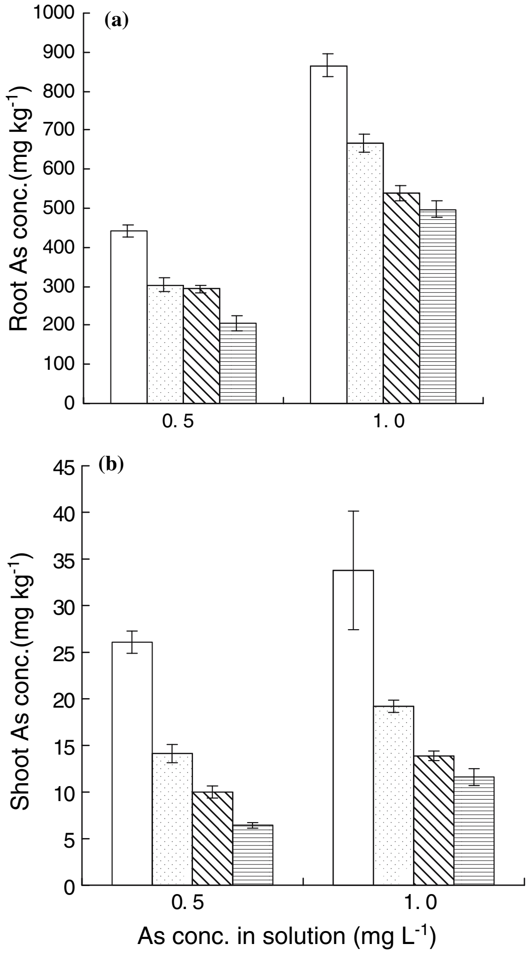

Figure 2. Mean As concentrations in roots (a) and shoots (b) of rice grown in nutrient solution with one of four Si levels and with one of three As levels. □, 0 mg Si L^{-1}; ▢, 14 mg Si L^{-1}; ▧, 28 mg Si L^{-1}; and ▤, 56 mg Si L^{-1}. Error bars: standard errors ($n = 4$).

1.0 mg L^{-1} significantly decreased root Si concentration (Figure 1b, $P = 0.005$).

As concentrations in shoots and roots increased significantly with increasing As levels in the nutrient solution (Figure 2a, b, $P < 0.001$). There was a highly significant Si × As interaction (Figure 2a b, $P < 0.001$), since increasing external Si concentration led to significant decreases in shoot and root As concentrations (Figure 2a, b, $P < 0.001$).

Shoot P concentration decreased significantly with increasing As and Si concentrations in the nutrient solution (Figure 3a, $P < 0.001$). There was a significant Si × As interactive effect observed on shoot P concentration (Figure 3a,

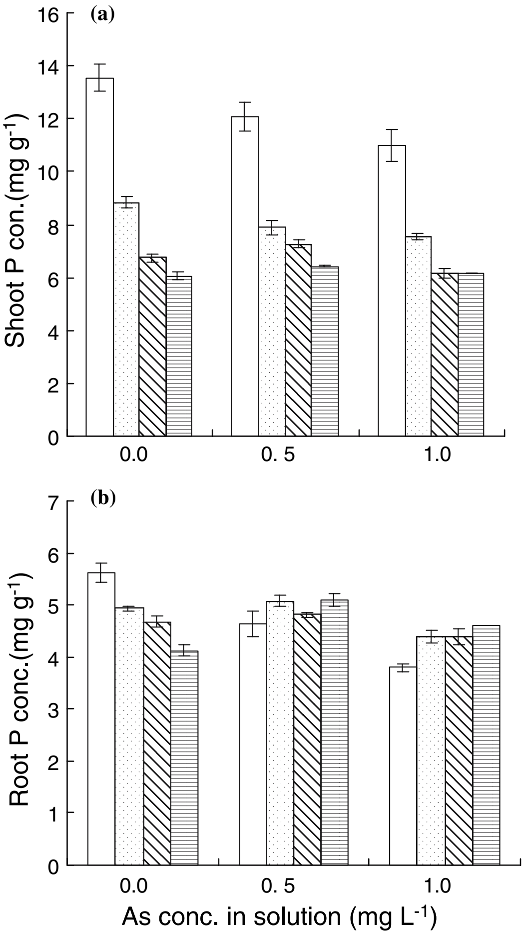

Figure 3. Mean P concentrations in shoots (a) and roots (b) of rice grown in nutrient solution with one of four Si levels and with one of three As levels. Symbols: see Figure 2. Error bars: standard errors ($n = 4$).

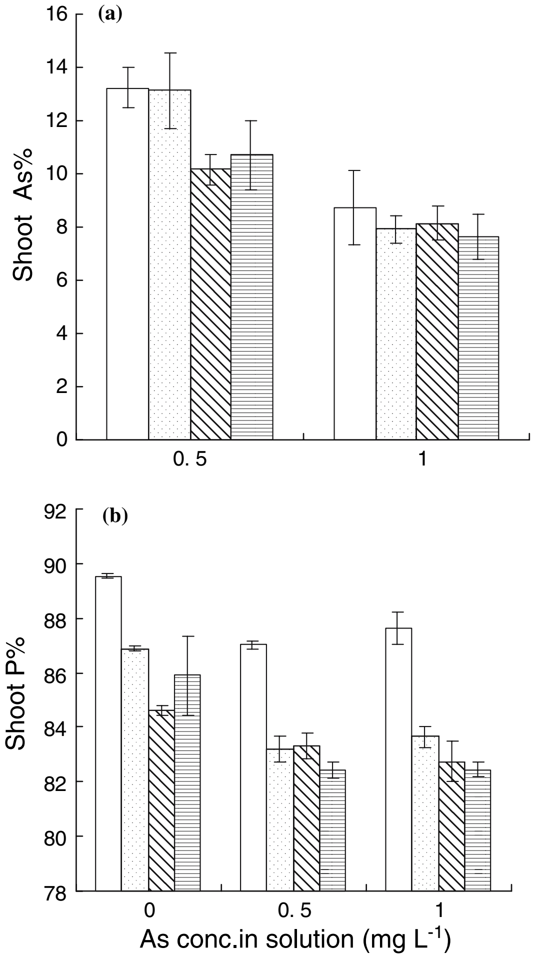

Figure 4. Mean As (a) and P (b) translocation to shoots of rice grown in nutrient solution with one of four Si levels and with one of three As levels. Symbols: see Figure 2. Error bars: standard errors ($n = 4$).

$P = 0.002$). Regardless of the As treatments, shoot P concentrations were reduced by 34, 45 and 49% in 14, 28 and 56 mg L^{-1} Si treatments, respectively (mean values for the three As treatments, $P < 0.001$). Furthermore, it is interesting to note that Si and As interactions inhibited shoot P concentration to a constant value of around 6 mg g^{-1} (Figure 3a).

The presence of Si in the nutrient solution reduced root P concentration in the zero-As treatment ($P < 0.001$), and had no effect on root P concentration in the other treatments (Figure 3b, $P = 0.54$). Addition of As at the rate of 0.5 mg L^{-1} did not affect root P concentration but at 1.0 mg L^{-1} significantly reduced root P concentration in the zero-Si treatment (Figure 3b, $P < 0.001$). There was a highly significant Si $\times$ As interactive effect observed on root P concentration (Figure 3b, $P < 0.001$).

As and P translocation from roots to shoots

The presence of Si in the culture solution did not affect As translocation from roots to shoots in any treatment (Figure 4a, $P = 0.18$). Increasing As concentration in the nutrient solution significantly reduced As translocation to shoots (Figure 4a, $P < 0.001$). There was a significant difference in P translocation from roots to shoots between the zero-As treatment and the As treatments (Figure 4b, $P < 0.001$), but no differences among the As treatments. Addition of Si to the

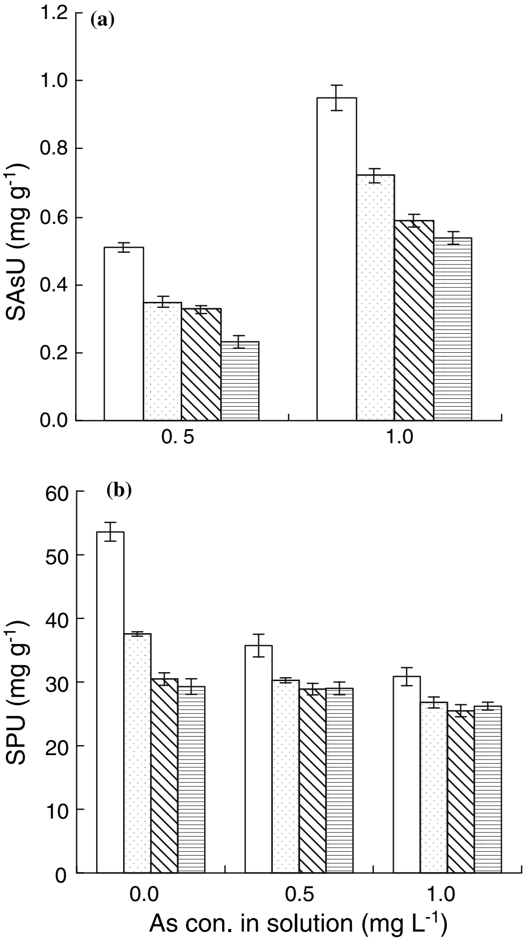

Figure 5. Mean specific As (a) and P (b) uptake by rice seedlings grown in nutrient solution with one of four Si levels and with one of three As levels. Symbols: see Figure 2. Error bars: standard errors ($n = 4$).

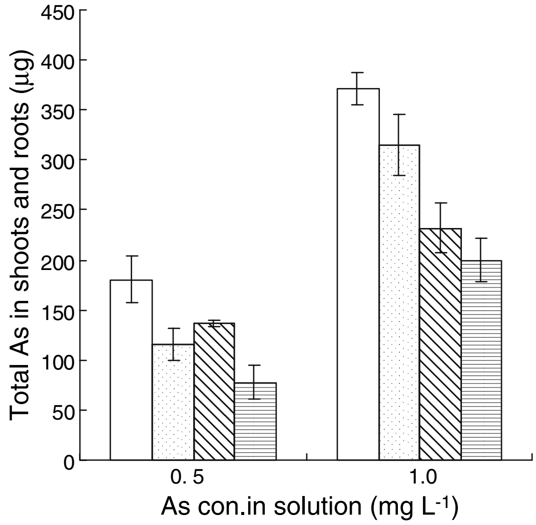

Figure 6. Mean total As in shoots and roots of rice grown in nutrient solution with one of four Si levels and with one of three As levels. Symbols: see Figure 2. Error bars: standard errors ($n = 4$).

culture solution significantly decreased P translocation from roots to shoots (Figure 4b, $P < 0.001$) and P translocation was similar among the Si treatments.

Specific As uptake (SAsU) *and Specific P uptake* (SPU)

Increasing Si concentration in the nutrient solution significantly reduced SAsU in all As treatments (Figure 5a, $P < 0.001$); while increasing As concentration in the solution significantly increased SAsU (Figure 5a, $P < 0.001$). There was a highly significant Si × As interaction for SAsU (Figure 5a, $P < 0.001$). SPU was significantly decreased by As and Si additions to the nutrient solution (Figure 5b, $P < 0.001$). There was a highly significant Si × As interaction for SPU (Figure 5b, $P < 0.001$).

Total As and P uptake

Increasing external As concentration increased the total As uptake by shoots and roots (Figure 6, $P < 0.001$) but the presence of Si in the growth solution significantly reduced total As uptake in roots and shoots (Figure 6, $P < 0.001$). Increasing external As concentration had no significant effect on root P uptake (Figure 7a, $P = 0.18$), but significantly reduced shoot P uptake (Figure 7b, $P = 0.05$). The presence of Si in the culture solution markedly reduced shoot P uptake (Figure 7b, $P < 0.001$) but had only a marginal effect on root P uptake in all treatments (Figure 7a, $P = 0.23$).

Discussion

Effect of Si and As on plant biomass

It is generally known that the application of Si is beneficial to the growth of rice plants both in the field and under glasshouse conditions (Liang et al., 1994; Ma and Takahashi, 1989, 1990; Ma et al., 1989; Okuda and Takahashi, 1964). Our

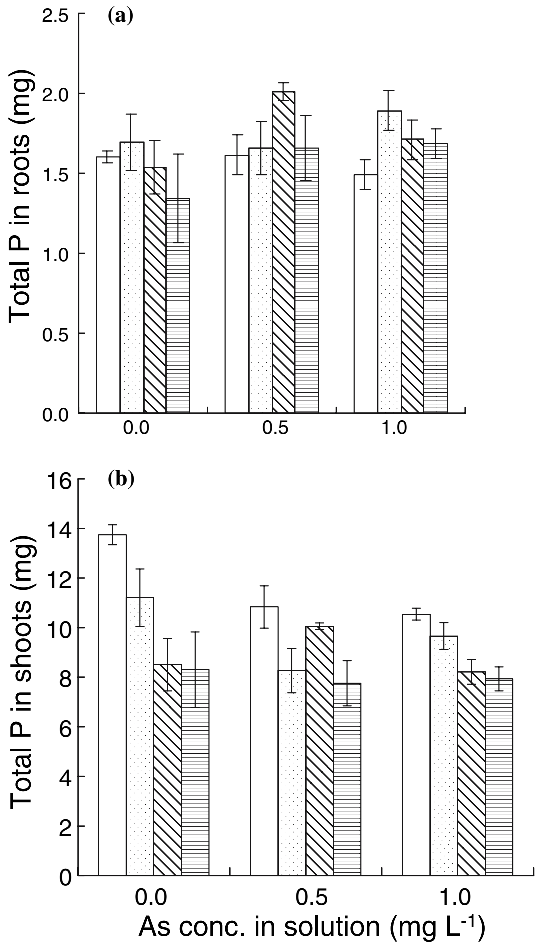

Figure 7. Mean total P in roots (a) and shoots (b) of rice grown in nutrient solution with one of four Si levels and with one of three As levels. Symbols: see Figure 2. Error bars: standard errors ($n = 4$).

results confirm this in that addition of Si to the nutrient solution significantly increased shoot dry weight (Table 1, $P = 0.001$). Effects of As on plant growth varied between As species, plant species and experimental conditions. Under our experimental conditions, addition of As to the culture solution did not affect shoot yield but slightly increased root dry weight compared to the zero-As control (Table 1, $P = 0.01$). Positive effects of As on root growth have also been reported for *Spartina alterniflora* in solution culture (Carbonell et al., 1998). The explanation for the positive growth response to As addition is unclear but may be related to P nutrition (Carbonell et al., 1998).

Effects of Si and As on plant P uptake

It is generally assumed that addition of Si to the culture medium will inhibit P accumulation by rice (Ma and Takahashi, 1989, 1990; Okuda and Takahashi, 1961a, b), and tomato, cucumber and soybean (Miyake and Takahashi, 1978, 1983, 1985). In the present experiment, shoot P concentrations were reduced substantially by the addition of Si to the nutrient solution, and this in agreement with previous reports. The mechanism of the inhibitory effect of Si on P uptake is not clear. It has been speculated that this effect may be due partly to the physiological substitution of silicate for phosphate, and that silicate may also compete directly with phosphate for plant uptake (Hall and Morison, 1906).

Numerous studies have shown reduction in phosphate uptake by plants due to arsenate (Asher and Reay, 1979; Jacobs and Keeney, 1970). Arsenate and phosphate are transported by the same uptake system, which has a higher affinity for phosphate than arsenate (Asher and Reay, 1979; Meharg and Macnair, 1990; Meharg et al., 1994). In the present experiment increasing As concentrations in the culture solution also reduced P concentrations in shoots and roots (Figure 3a, b, $P < 0.001$). Nevertheless, As inhibited shoot P concentration to a smaller extent than Si. The observed decrease in P translocation from roots to shoots in the treatments with As addition could be due to the slight increase in root biomass with As application.

It is interesting to note that the interactions between Si and As inhibited shoot P concentration to a constant value of around 6 mg g^{-1} (Figure 3a). There may be two possible explanations: (1) P concentrations in the plants decreased significantly with increasing Si and As levels in the nutrient solution. Since As can substitute for P within the plants but is unable to carry out the same physiological functions as P, the plant therefore reacts as if there is a P deficiency (Burló et al., 1999; Carbonell et al., 1998). Thus, as plant As concentrations increase, the plant reacts by increasing P uptake to maintain a constant P concentration; and (2) P uptake by the plants was mediated by a negative feedback mechanism for assessing the P status of the whole plant and for transmitting a systemic signal via the shoots to all parts of the root system

(Daram et al., 1998; Leggewie et al., 1997; Liu et al., 2001; Smith, 2001). The physiological functioning of cells requires that P concentrations in the cytosol be maintained within a narrow range (Mimura et al., 1996). When the P concentration in the plants is lower than the normal range, the plants increase P uptake through the feedback mechanism. Thus, the increase in P uptake via the negative feedback mechanism maintains a constant P concentration to fulfill the normal physiological functioning of cells.

Effect of Si on As uptake

In our study As concentrations in rice plants depended on the level of As and Si in the culture solution. External Si application lowered the As concentrations in shoots and roots (Figure 2a, b, $P < 0.001$). Simultaneously, the addition of Si led to a decline in shoot P concentration (Figure 3a, $P < 0.001$). These results show that increasing Si in the culture solution produced a similar degree of reduction in shoot As and P concentrations. Until now, few studies have been conducted to elucidate the mechanism by which Si decreases As uptake. We may speculate that the mechanism by which Si decreases As and P uptake by rice plant may be related to the interactions between As and P. However, further experiments will be required to elucidate the mechanisms by which Si inhibits As uptake by rice seedlings at both the physiological and molecular levels.

In conclusion, our results demonstrate that applying Si to the growth medium markedly decreased As concentrations in the shoots and roots and total As uptake by rice seedlings. In addition, Si significantly decreased shoot P concentration and uptake. Based on these results, it can be concluded that increasing Si concentrations in the culture medium may provide a viable approach for reducing As accumulation in rice grown in As contaminated soils, but field studies are required to confirm this.

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