Rhizosphere characteristics of two arsenic hyperaccumulating *Pteris* ferns

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Better understanding of the processes controlling arsenic bioavailability in the rhizosphere is important to enhance plant arsenic accumulation by hyperaccumulators. This greenhouse experiment was conducted to evaluate the chemical characteristics of the rhizosphere of two arsenic hyperaccumulators *Pteris vittata* and *Pteris biaurita*. They were grown for 8 weeks in rhizopots containing arsenic-contaminated soils (153 and 266 mg kg⁻¹ arsenic). Bulk and rhizosphere soil samples were analyzed for water-soluble As (WS-As) and P (WS-P), pH, and dissolved organic carbon (DOC). Comparing the two plants, *P. vittata* was more tolerant to arsenic and more efficient in arsenic accumulation than *P. biaurita*, with the highest frond arsenic being 3222 and 2397 mg kg⁻¹. Arsenic-induced root exudates reduced soil pH (by 0.74–0.92 units) and increased DOC concentrations (2–3 times) in the rhizosphere, resulting in higher WS-P (2.6–3.8 times higher) compared to the bulk soil. Where there was no difference in WS-As between the rhizosphere and bulk soil in soil-153 for both plants, WS-As in the rhizosphere was 20–40% higher than those in bulk soil in soil-266, indicating that the rate of As-solubilization was more rapid than that of plant uptake. The ability to solubilize arsenic via root exudation in the rhizosphere and the ability to accumulate more P under arsenic stress may have contributed to the efficiency of hyperaccumulator plants in arsenic accumulation.

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1. Introduction

Arsenic-contaminated soils are of great concern worldwide due to arsenic’s toxicity as a carcinogen (Ma et al., 2001). Phytoextraction has the potential to be used to clean up arsenic-contaminated soils. It uses plants that hyperaccumulate arsenic in the aboveground biomass, which can be harvested and removed from soils. Identification of As hyperaccumulators, such as fern species in the *Pteris* genus (Ma et al., 2001; Srivastava et al., 2006), makes phytoextraction of arsenic-contaminated soils a viable technology.

However, improving the efficacy of phytoextraction technique is critical for its successful application in arsenic-contaminated soils. For instance, phytoextraction can be enhanced through plant-facilitated solubilization of arsenic in soil and subsequently uptake by hyperaccumulator plants (Huang et al., 1998; Chen and Cutright, 2001). Many studies investigated factors regulating the growth of those hyperaccumulating plants for maximum As removal from contaminated sites (Tu and Ma, 2003). However, processes that regulate arsenic hyperaccumulation phenomenon have not yet been fully elucidated. Even though rhizosphere processes are well studied in crop plants (Hinsinger et al., 2003; Darrah et al., 2006; Hinsinger and Marschner, 2006), gaps exist as far as hyperaccumulators are concerned. Moreover, the mechanisms of how hyperaccumulator plants solubilize and take up As from contaminated soils are still unclear.

The rhizosphere is a dynamic region where multiple interactive processes take place (Darrah et al., 2006). Root architecture and physiology, root-induced changes in water and nutrient availability, root exudates, and fungal and bacterial associations (Gahoonia and Nielsen, 2003) are all components of the dynamic rhizosphere system. Unraveling those plant root–soil–microbe interactions in the rhizosphere is central to many areas such as plant nutrition, ecosystem diversity, rehabilitation of degraded soil, water quality, and bioremediation including phytoextraction (Hinsinger and Marschner, 2006).

Root–soil interactions in the rhizosphere play a key role in controlling nutrient availability to plants (Hinsinger, 2003). Fitz and Wenzel (2002) reported that root-induced changes in the rhizosphere altered its chemical composition and facilitated arsenic uptake by *Pteris vittata* L (Chinese brake fern), the first-known arsenic hyperaccumulator. Dissolved organic carbon (DOC) present in root exudates such as carboxylic acids is involved in mobilizations of inorganic P in the rhizosphere by changing soil pH, displacing P from sorption sites, catalyzing P-immobilizing metal cations and forming soluble metal chelate complexes with P (Kirk et al., 1999). These...
2.1. Plant propagation and soil characterization of arsenic uptake by As-hyperaccumulating rhizosphere, as well as their ability to accumulate As in the biomass.

Processes also affect As availability since arsenate is an analog of phosphate (Adriano, 2001). Therefore, competition for sorption sites between these two elements in soils (Adriano, 2001) increases each other’s availability (Manning and Goldberg, 1996; Smith et al., 2002).

Another factor that controls the availability of trace metals, including As, is soil pH (Fitz and Wenzel, 2002). Changes in rhizosphere pH can be up to 2 units compared with the bulk soil and may enhance As bioavailability, thereby increasing As uptake by plants (Tu et al., 2004).

In addition to P. vittata, another arsenic hyperaccumulating fern Pteris biaurita L. has been identified (Srivastava et al., 2006). The present study was conducted to 1) compare the changes in pH and DOC in the rhizosphere of the two hyperaccumulators; and 2) examine how those parameters influence As and P availability in the rhizosphere, as well as their ability to accumulate As in the biomass. The results of this study may help to better understand the key aspects of arsenic uptake by As-hyperaccumulating Pteris ferns and optimizing management practices for maximum arsenic phytoextraction.

2. Material and methods

2.1. Plant propagation and soil characterization

P. vittata and P. biaurita plants used in the study were propagated in our laboratory (Jones, 1987). Uniform plants, with similar height and number of fronds were used. The soils used in this study (sandy, siliceous, hyperthermic grossarenic paleudult) were collected from an abandoned site in north central Florida. The site was contaminated with arsenic from using chromated-copper-arsenate (CCA) for wood preservation between 1951 and 1962. (Komar, 1999).

The soil pH was measured using a 1:2 soil to water ratio; cation exchange capacity was determined by an ammonium acetate method (Thomas, 1982); organic matter content was measured by the Walkley Black method (Nelson and Sommers, 1982); and particle size was measured by the pipette method (Day, 1965). Selected physical and chemical properties of the soil are summarized in Table 1.

2.2. Experimental design

A greenhouse experiment was set up as a 2 × 2 × 2 split–split plot with randomized replication. The main plot consisted of two fern species (P. vittata and P. biaurita), which were cultivated in soils containing two As concentrations (153 mg kg⁻¹ and 266 mg kg⁻¹) as sub plot. Upon completion, the bulk and rhizosphere soil, sub–sub plots were evaluated. Each treatment was replicated four times.

The two soils were air-dried and sieved (2 mm). 2.5 kg of soil were thoroughly mixed with 3.0 g of Osmocote, an extended time-release base fertilizer (18–6–12) (Scotts-Sierra Horticultural Products Co., Marysville, OH), and then poured into a plastic rhizopot (16 cm in height and 15 cm in diameter; Gonzaga et al., 2006), with 500 g in the rhizosphere and 2000 g in the bulk soil. Plastic frames (13 cm in height and 7 cm in diameter) covered with 45 µm nylon mesh cloth were used to separate the rhizosphere from the bulk soil in the rhizopot. Root growth was limited to the central compartment within the nylon cloth. One week before the study, the soil was set to equilibrate at field capacity. One healthy fern with six fronds was transplanted into each pot.

The plants were allowed to grow for 8 weeks in a greenhouse with an average night/day temperature of 14/30 °C and an average photosynthetically active radiation flux of 825 µmol m⁻² s⁻¹. The plants were watered throughout the study to keep the soil at approximately 70% of its field capacity.

At the end of the experiment, the ferns were harvested and each plant was separated into roots and fronds. The plants were washed thoroughly with tap water and then rinsed with distilled water. The fronds were oven dried for 3 days at 65 °C, weighed, and ground using a Willey mill to 60-mesh fineness for chemical analysis.

Rhizosphere (soil attached to the roots obtained through gently shaking the roots) and bulk soils (soil outside the central compartment) were separated. They were sieved and analyzed for arsenic, phosphorus, soil pH and DOC.

2.3. Chemical analysis

Rhizosphere and bulk soil were evaluated for water-soluble arsenic and phosphorus, and DOC in 1:4 soil to water ratio (Olsen et al., 1982), obtained after shaking (1 h), centrifuging (15 min at 3500 × g) and filtering (0.45 µm syringe filter). Water-soluble As was determined with graphite furnace atomic absorption spectrophotometry (GFAAS, SIMMA 6000; PerkinElmer, Norwalk, CT). Water-soluble P was determined by a modified molybdenum blue method (Carvalho et al., 1998). This involved reducing arsenic in solutions from As (V) to As (III) with L-cysteine to remove arsenic interference with the phosphate analysis.

The concentration of DOC was measured using a TOC-5050A TOC analyzer (Shimadzu). Soil pH was measured using a 1:2 soil to water ratio. Plants and soils were digested using EPA Method 3050A for the Hot Block Digestion System (Environmental Express, Mt. Pleasant, SC) and then determined using GFAAS. Quality control of arsenic analysis was included using standard reference materials 1547 (peach leaves) and 2710 (soil) (US NIST, MD) with arsenic recovery of 100 ± 20%.

2.4. Data analysis

Plant and soil effects were statistically tested for significance by analyses of variance according to the generalized linear model procedure of the statistical analysis system (SAS Institute Inc. 1987). Treatment means were separated by Duncan’s multiple range tests using a level of significance of p < 0.05.

3. Results and discussion

This greenhouse experiment determined the rhizosphere characteristics (pH, DOC, and water-soluble and total P and As) of two arsenic hyperaccumulators (P. vittata and P. biaurita) after growing in two arsenic-contaminated soils (soil-153 and soil-266) for 8 weeks. In addition, arsenic and P concentrations in the fronds and roots of the ferns were determined.
and P. ryukyuensis are arsenic hyperaccumulators (reported root P:As ratios of 13–27 and frond P:As ratios of 2.7–4.8 for four arsenic hyperaccumulators (P. biaurita, P. cretica, P. quadriaurita, and P. ryukyuensis) after growing for 6 weeks in a soil spiked with 100 mg As kg\(^{-1}\). The ability of arsenic hyperaccumulators to keep high P/As ratios in the biomass, especially in the roots, helps them to tolerate arsenic (Tu and Ma, 2004).

### 3.3. Water-soluble arsenic and P were higher in the rhizosphere

Water-soluble (WS) arsenic and P are good indicators of their bioavailability for plant uptake from a soil (McBride, 1994) since plants preferentially take up nutrients from the soil solution (Linehan et al., 1985). The capacity of a soil to sustain the concentration of a particular ion in solution during plant growth depends upon the balance between the two opposite processes: solubilization of the ion from soils and its uptake by plants. Solubilization may be facilitated by release of organic acids and reduction in pH. When plant uptake is more rapid than solubilization from the soils, solution As and P concentrations will be reduced.

Since the two soils had different total arsenic (153 and 266 mg kg\(^{-1}\); Table 1), no comparison was made between the two soils. For soil-153, there was no difference in WS-As between the two plants or the two

#### Table 2

Plant biomass, arsenic and phosphorus concentration and accumulation, and P:As molar ratio of P. vittata and P. biaurita after growing for 8 weeks in two As-contaminated soils containing 153 and 266 mg kg\(^{-1}\) As.

<table>
<thead>
<tr>
<th>Plant parameters</th>
<th>Soil-153</th>
<th>Soil-266</th>
</tr>
</thead>
<tbody>
<tr>
<td>Constant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Frond biomass (g)</td>
<td>15.3 (^{1})</td>
<td>15.9 a</td>
</tr>
<tr>
<td>Root biomass (g)</td>
<td>3.4 a</td>
<td>3.00 a</td>
</tr>
<tr>
<td>Root P (mg pot(^{-1}))</td>
<td>41.0 a</td>
<td>20.0 b</td>
</tr>
<tr>
<td>Root As (mg kg(^{-1}))</td>
<td>4.53 b</td>
<td>5.72 a</td>
</tr>
<tr>
<td>Root P (g kg(^{-1}))</td>
<td>1.51 a</td>
<td>1.29 a</td>
</tr>
<tr>
<td>Root As (g mg pot(^{-1}))</td>
<td>0.14 a</td>
<td>0.06 b</td>
</tr>
<tr>
<td>Root P (mg pot(^{-1}))</td>
<td>69.4 b</td>
<td>90.7 a</td>
</tr>
<tr>
<td>Root As (mg kg(^{-1}))</td>
<td>5.10 a</td>
<td>3.90 a</td>
</tr>
<tr>
<td>Frond P (g kg(^{-1}))</td>
<td>6.74a</td>
<td>5.06b</td>
</tr>
<tr>
<td>Frond As (mg kg(^{-1}))</td>
<td>74.5a</td>
<td>94.6a</td>
</tr>
</tbody>
</table>

Means followed by the same letter for a given soil were not significantly different by Duncan test at \(p<0.05\).

### 3.1. P. vittata was more tolerant to arsenic and more efficient in arsenic accumulation

During the 8-week growth, no visual symptoms of As toxicity were observed for the two ferns growing in arsenic-contaminated soils. The frond and root biomass of P. vittata was not affected by soil As concentration. In contrast, the frond and root biomass of P. biaurita was reduced by 20% when soil arsenic increased from 153 to 266 mg kg\(^{-1}\) (soil-153 to soil-266) (Table 2). After growing in soil-153 and soil-266 for 8 weeks, the arsenic concentrations in P. vittata fronds were 426 and 3222 mg kg\(^{-1}\), and those in the roots were 410 and 373 mg kg\(^{-1}\) (Table 2). The corresponding numbers for the fronds and roots of P. biaurita in the two soils were 316 and 2397 mg kg\(^{-1}\), and 20.0 and 289 mg kg\(^{-1}\). P. vittata fronds accumulated 66 and 51 mg As pot\(^{-1}\), and P. biaurita fronds accumulated 5.0 and 31 mg As pot\(^{-1}\) from soil-153 and soil-266, respectively. These values were 98% greater than those in the roots of P. vittata and P. biaurita.

Comparing the two ferns, P. vittata accumulated significantly more arsenic in the fronds (32–61%) and the roots (32–133%) than P. biaurita (\(p<0.05\)) from the two soils. Comparing the two soils, the two ferns took up 8–15 times more arsenic from soil-266 than soil-153 though the difference in total arsenic was only 74% and Melhich-III-extractable As was 42% (Table 2). It is unclear as to why the ferns took up so much more arsenic from soil-266 than soil-153 since the two had similar physical and chemical properties (Table 1). However, the remarkable ability of the two Pteris ferns to bioconcentrate arsenic makes them good candidates to be used to remediate As-contaminated soils.

### 3.2. Both plants had greater P:As ratios in the roots than fronds

Similar to other plant species (Asher and Reay, 1979), both arsenate and P are taken up by P. vittata via the phosphate transport systems (Meharg and Hartley-Whitaker, 2002). Though both P. vittata and P. biaurita are arsenic hyperaccumulators, they accumulated more P than As in their biomass (Table 2), which is consistent with previous report (Tu and Ma, 2003). The molar ratios of P:As in the fronds were 26–44, and 8.2–8.6 in soil-153 and soil-266, whereas the corresponding numbers for the roots were 90–156, and 10–15, respectively. Compared to the fronds, the molar ratios of P:As in the roots were greater, e.g. 3.4–3.6 times in soil-153 and 1.2–1.5 times in soil-266. These results are similar to those of Srivastava et al. (2006). They reported root P:As ratios of 13–27 and frond P:As ratios of 2.7–4.8 for four arsenic hyperaccumulators (P. biaurita, P. cretica, P. quadriaurita and P. ryukyuensis) after growing for 6 weeks in a soil spiked with...
compartment (Fig. 1a). However, for soil-266, WS-As in the rhizosphere soil was 33% (P. vittata) and 72% (P. biaurita) greater than those in bulk soil. This means that in soil-266, the amounts of arsenic solubilized exceeded the arsenic uptake ability of both plants.

Unlike WS-As, for both plants and soils, WS-P concentrations were significantly higher in the rhizosphere than those in the bulk soil (Fig. 1b), indicating P solubilization is faster than P uptake by plants. For soil-153, the WS-P concentrations in the rhizosphere were 3.0–3.8 times higher than those in the bulk soil. For soil-266, they were 2.2–2.6 times greater. Compared the rhizosphere soils, opposite trends were observed for the two plants. While P. biaurita had greater WS-P in soil-153 (6.4 vs. 4.0 mg kg\(^{-1}\)), P. vittata had greater WS-P in soil-266 (7.2 vs. 5.3 mg kg\(^{-1}\)). The increase in rhizosphere WS-P and WS-As (compared to bulk soil) indicated that the solubilization process was plant driven.

3.4. Arsenic-induced root exudation reduced pH and increased DOC in the rhizosphere

The soil pH ranged from 6.38 to 7.41, which was well in the range of greater availability of the two oxyanions (As and P) in the system.

Table 3

<table>
<thead>
<tr>
<th>Soil parameter</th>
<th>pH</th>
<th>DOC</th>
<th>WS-As</th>
<th>WS-P</th>
<th>Arsenic accumulation</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>0.781**</td>
<td>0.958***</td>
<td>-0.002</td>
<td>0.544**</td>
<td></td>
</tr>
<tr>
<td>DOC</td>
<td>-</td>
<td></td>
<td>-0.037</td>
<td>0.601***</td>
<td></td>
</tr>
<tr>
<td>WS-As</td>
<td>-</td>
<td></td>
<td>-</td>
<td>-0.413***</td>
<td></td>
</tr>
</tbody>
</table>

*p<0.05, **p<0.01 and ***p<0.001.

No change in pH was observed in the bulk soil or in the rhizosphere soil between two plants (Fig. 2a). Therefore, the changes observed in the rhizosphere were root-induced. Both plant species acidified the rhizosphere. For instance, the rhizosphere pH was 0.74–0.76 (soil-153) and 0.89–0.92 (soil-266) units lower than those in the bulk soil.

Since both As and P are present as oxyanions in soils, their uptake by plants should increase rhizosphere pH. This is because, to balance charges, after taking up As and P, plants will release OH\(^{-}\) into the rhizosphere. The reduction in pH was probably due to increased release of root exudates, acidifying rhizosphere soil to release both As and P. This was consistent with greater DOC concentrations in the rhizosphere soils for both plants and soils.

The DOC concentrations in the rhizosphere of both fern species were 2–3 times greater than those in the bulk soil (Fig. 2b). Differences were also observed between the rhizosphere soils between the two fern species. Greater As concentration in the soil resulted in greater DOC for both plants (Table 3), indicating As-induced plant release of root exudates.

Fitz and Wenzel (2002) proposed that hyperaccumulators may enhance metal solubility in the rhizosphere via root exudation, consequently increasing plant metal uptake. Our experiment seemed to support this hypothesis since the more efficient hyperaccumulator P. vittata exuded 19–45% more DOC in the rhizosphere than did P. biaurita in both soils (Fig. 2b). The high correlation between rhizosphere DOC and WS-As (r = 0.781), and rhizosphere DOC and plant arsenic accumulation (r = 0.911) was consistent with the hypothesis (Table 3).

Tu et al. (2004) demonstrated that when exposed to higher arsenic in the solution, P. vittata released more root exudates. This is probably due to arsenic-induced P deficiency since they are chemical analogs. We would expect higher DOC concentrations in the rhizosphere of soil-266 than soil-153, which was the case (Fig. 2b). While there were no differences in DOC concentrations in the bulk soils, the DOC concentrations in the rhizosphere of P. vittata and P. biaurita in soil-266 were 40 and 15% greater than those in soil-153 (Fig. 2b).

3.5. Arsenic availability and plant uptake in relation to P, soil pH and DOC

Concentrations of Mehlich-III-extractable As (43.7 and 61.9 mg kg\(^{-1}\)) were higher than those of P (28.8 and 269 mg kg\(^{-1}\)) in soil-153 and soil-266 (Table 2). This was consistent with the concentrations of WS-As and P in the two soils (Fig. 1).

Soil pH is considered to be one of the most important chemical factors controlling the availability of heavy metals (Fitz and Wenzel, 2002). Usually, the rhizosphere is viewed as an acidified soil component compared to the bulk soil, however, depending on the nutritional status of a plant, alkalinization can also be observed (Nye, 1981). Reduction in rhizosphere pH increases the chemical activity of most metals (Lindsay, 1979), thereby increasing As uptake by the ferns (Tu et al., 2004). Both plant species had higher DOC concentrations in the rhizosphere as compared with the bulk soil (Fig. 2b).

![Figure 2](image-url)

Fig. 2. pH (a) and concentrations of dissolved organic carbon (b) in the bulk soil and rhizosphere of P. vittata and P. biaurita after 8 weeks of growth in two As-contaminated soils containing 153 and 266 mg As kg\(^{-1}\). Control = pots without plants. Bars represent standard deviations of four replicates. Means followed by the same uppercase letter (two soil compartments for a given plant), and lowercase letter (two plants for a given soil compartment) are not significantly different. The analyses were done using Duncan test at p<0.05.
The presence of organic molecules and inorganic oxyanions may compete with As for sorption sites, thus reducing As sorption to mineral surfaces and increasing As bioavailability in soils (Manning and Goldberg, 1996; Grafe et al., 2001). Despite the fact that DOC accounts for a small portion of total OC, it significantly affects nutrient and contaminant mobility, microbial activity and soil properties (Haynes, 2000). The change in rhizosphere DOC concentration may have further implications with respect to the availability of nutrients and soil microbial population (Kullberg et al., 1993). In general, DOC readily forms both aqueous and surface inner-sphere complexes with cationic metals and metal oxides, which, in turn, may associate strongly with other dissolved anions by metal-biding mechanisms (Thanabalasingam and Pickering, 1986), diminishing the tendencies of such anions to form surface complexes. Thus, the reaction of DOC with arsenic is highly expected and has the potential to influence arsenic sorption and mobility.

The main sources of DOC in soils are plant litter, soil humus, and root exudates (Kalbitz et al., 2000). It has been reported that P. vittata releases various low molecular weight organic acids (Tu et al., 2004) via root exudation. The presence of these acids may significantly influence As and P mobilization in the rhizosphere. A more pronounced effect of DOC is expected in low buffered soil, such as the sandy soil used in this study, which had low organic matter (1.1%–1.3%) and low clay content (2.7%–2.8%) (Table 1).

Increase in WS-As in P. vittata rhizosphere was reported in other studies. Fayiga et al. (2004) also observed an increase of 10–22 times in soil WS-As after growing P. vittata in an arsenic-contaminated soil for 5 weeks. However, depletion of available P in the rhizosphere is a common situation for most plants given the transport characteristics of P in soil.

In the present study, WS-P and DOC played important roles in WS-As availability. Increasing both WS-P (r = −0.968, p = 0.0015) and DOC (r = −0.985 p = 0.0003) reduced rhizosphere WS-As in P. vittata, as indicated by the correlation coefficients, while increase in WS-P (r = 0.871, p = 0.0239) and DOC (r = 0.974, p = 0.0010) increased the WS-As in P. biaurita. The apparent discrepancy in behavior on the rhizosphere of the two species may be accounted by the difference in their ability to accumulate arsenic. P. vittata accumulated 25% more As from soil-153 and 38% more As from soil-266 than P. biaurita. Thus, a greater concentration of WS-As in the rhizosphere of P. biaurita reflects a reduced ability of the species to take up the available As in soil-266.

Despite the species’ influence on WS-As mobilization in the rhizosphere, this more labile As accounted for < 1.2% of the total As accumulated by plants. If the WS-As from the bulk soil was the primary supply of the rhizosphere As, it would account for an additional 50.0%–55.2 and 68.6–88.0% of the As accumulated by P. vittata and P. biaurita from the two soils. Hence, about 50% of As accumulated by P. vittata was from less available pool while for P. biaurita it was 15–30% for the two soils.

Arsenate and phosphate are chemical analogues and both are taken up via phosphate transport systems in P. vittata (Meharg and Hartley-Whitaker, 2002) similar to other plant species (Asher and Reay, 1979). Phosphorus concentrations in the plants growing in soil-266 (P vittata = 1.08% and P biaurita = 0.86%) were about 2 and 1 fold greater than those in soil-153 (0.46 and 0.57%, respectively). Higher plant phosphorus may also have played a role in As accumulation in Pteris ferns.

4. Conclusions

P. vittata was more efficient in arsenic accumulation than P. biaurita. Root-induced pH reduction and DOC increase helped to solubilize As and P from the rhizosphere since WS-As and WS-P accounted for < 1% of the As and P taken up by the plants. A depletion of solution arsenic was observed in the rhizosphere of P. biaurita and P. vittata when grown in soil-153 with lower WS-As, showing that the rate of uptake was higher than that of arsenic solubilization. The ability of the two As hyperaccumulators to produce more root exudates in the rhizosphere and accumulate more P inside the plants under increased arsenic stress may have helped them to accumulate more arsenic.

Acknowledgments

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