Mechanisms of efficient As solubilization in soils and As accumulation by As-hyperaccumulator *Pteris vittata*

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**Abstract**

Arsenic (As) in soils is of major environmental concern due to its ubiquity and carcinogenicity. *Pteris vittata* (Chinese brake fern) is the first known As-hyperaccumulator, which is highly efficient in extracting As from soils and translocating it to the fronds, making it possible to be used for phytoremediation of As-contaminated soils. In addition, *P. vittata* has served as a model plant to study As metabolisms in plants. Based on the recent advances, we reviewed the mechanisms of efficient As solubilization and transformation in rhizosphere soils of *P. vittata* and effective As uptake, translocation and detoxification in *P. vittata*. We also provided future research perspectives to further improve As phyto remediation by *P. vittata*.

**1. Introduction**

Due to its ubiquity and carcinogenicity, arsenic (As) has received much attention (Chakraborti et al., 2015). Its abundance ranks 20th in the Earth’s crust, averaging ~5 mg kg<sup>-1</sup> (Bissen and Frimmel, 2003; Lampis et al., 2015). Anthropogenic release from mining, smelting, and coal combustion activities has elevated its contents in the environment, posing risks to human health (Santi, 2013; Sun et al., 2016).

In soils, As primarily exists as inorganic arsenate (AsV) and arsenite (AsIII). While AsV mainly exists in aerobic soils, AsIII predominates in anaerobic soils, like flooded paddy soils (Bissen and Frimmel, 2003). Anthropogenic release from mining, smelting, and coal combustion activities has elevated its contents in the environment, posing risks to human health (Santi, 2013; Sun et al., 2016).

In soils, As primarily exists as inorganic arsenate (AsV) and arsenite (AsIII). While AsV mainly exists in aerobic soils, AsIII predominates in anaerobic soils, like flooded paddy soils (Bissen and Frimmel, 2003). Arsenite is more mobile and can be more toxic to plants than AsV (Zheng et al., 2013). Methylated As has also been found in soils, with common species including monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA) (Huang et al., 2011a).

Arsenic toxicity to living organisms varies with As species. In general, AsIII is more toxic than AsV, and inorganic As is more toxic than organic MMA and DMA (Shen et al., 2013). As a P analogue, AsV can inhibit oxidative phosphorylation, affect ATP synthesis, and disrupt energy generation (Bissen and Frimmel, 2003; Mead, 2005). Arsenite has a high affinity for sulfydryl (–SH) groups, which may affect enzyme activities and suppress metabolic processes (Tsai et al., 2009). In addition, AsIII can bind with glutathione (GSH) directly, leading to DNA and cell damage due to elevated reactive oxygen species (ROS) (Shen et al., 2013).

Arsenic contamination in soils threatens human health, especially for those who live in contaminated areas and have a considerable As-contaminated food intake (Smedley and Kinniburgh, 2013; Wang et al., 2015). As a remediation technology, plant-based phytoextraction of As from soils has attracted much attention recently (Kumar et al., 2015; Roy et al., 2015). The first known As-hyperaccumulator *Pteris vittata* (Chinese brake fern) was reported by Ma et al. (2001), making it possible for phytoremediation of As-contaminated soils. The fern has a staggering ability to extract As from soils, with frond As concentrations being as high as 23 g kg<sup>-1</sup> (Ma et al., 2001). Due to its high efficiency in As accumulation, *P. vittata* has been used to remediate As-contaminated soils (Kertulis-Tartar et al., 2006; Lessl et al., 2014).
and waters (Huang et al., 2004; Natarajan et al., 2011; Tu et al., 2004b). Besides, this fern has also been used as a model plant to study As uptake and detoxification in plants during the past 15 years (Danh et al., 2014; Chen et al., 2017). Though advances have been made in this area (Ali et al., 2009; Zhao et al., 2010a), the mechanisms of As-hyperaccumulation used by *P. vittata* are still not fully elucidated.

In this context, this article reviews the mechanisms of As solubilization and transformation in rhizosphere soils of *P. vittata*, which is important for phytoremediation of As-contaminated soils. This review also focuses on the mechanisms of efficient As uptake, translocation and detoxification in *P. vittata*. To better understand As-hyperaccumulation by *P. vittata*, the current knowledge gaps and future research perspectives are also provided.

2. Arsenic solubilization and transformation in rhizosphere soils

2.1. Arsenic solubilization in rhizosphere soils

In soils, AsV and P often bind with Fe to form insoluble minerals, reducing their availability (Fayiga and Ma, 2005; Sharma and Sohn, 2009). *P. vittata* grows well in alkaline soils where As, Fe and P are not readily available (Fig. 1) (Matschullat, 2000). The fact that *P. vittata* can extract large amounts of As from soil suggests it may have evolved strategies to mobilize hazardous element As and nutrient elements Fe and P.

To obtain sufficient nutrients (e.g., Fe and P) to sustain growth under nutrient-deficient and/or metal-stress conditions, plant roots often excrete organic acids to solubilize nutrients from poorly-soluble sources (Fig. 1) (Bais et al., 2006). Organic acids increase soluble P concentration via dissolving minerals and desorbing P from mineral surfaces (Ryan and Delhaize, 2001). Organic acids can compete with P for binding sites in soils by forming stronger complexes with AI, Fe, and Ca than does P. For example, P can be liberated from Ca-P minerals as organic acid complex with Ca or block P sorption onto other charged sites (Fu et al., 2017). For *P. vittata*, it can effectively utilize sparingly-soluble P sources, such as phosphate rock in soils, via producing root exudates, resulting in 33–39% more biomass than treatment with P fertilizer (Lessl and Ma, 2013). Organic acids can also replace the P bound to Fe or Al oxohydroxides via ligand exchange (Liu et al., 2017a). In these processes, organic acids play an important role in solubilizing P-bearing minerals by *P. vittata*, similar to other plants during P acquisition (Fig. 1) (Lessl and Ma, 2013; Liu et al., 2016). However, different from other plants that produce typical siderophores, which showed greater efficiency in FeAsO₄ dissolution than hydroxamate DFOB. Given the effectiveness of bacteria-produced siderophore in Fe solubilization (Das et al., 2014; Ghosh et al., 2015a), it is possible that As-resistant rhizobacteria is important for Fe acquisition and As accumulation in *P. vittata*.

In addition, as an analogue of P, As is also mobilized by P solubilization bacteria, leading to enhanced P and As uptake by plants, including *P. vittata* (Ghosh et al., 2011, 2015a). More recently, Liu et al. (2015) reported a catecholate-type siderophore produced by rhizobacteria of *P. vittata*, which showed greater efficiency in FeAsO₄ dissolution than hydroxamate DFOB. The effectiveness of bacteria-produced siderophore in Fe solubilization from Fe-As minerals, it is possible that As-resistant rhizobacteria are important for Fe acquisition and As accumulation in *P. vittata*.

2.2. Arsenic transformation in rhizosphere soils

In addition to As solubilization, microbes can also alter As speciation via oxidation and reduction (Figs. 1 and 2) (Fitz and Wenzel, 2002). Generally, As in soils is mainly present as AsV under oxidizing conditions (e.g., aerobic soils) and as AsIII under reducing conditions (e.g., flooded paddy soils) (Santi, 2013). However, in paddy soils, the abundance of As-oxidizing bacteria with AsIII oxidase gene (*aroA* and *flxR*) and AsV respiratory reductase gene (*arox*), indicating the dominance of microbial As oxidation, though some AsIII can be detected (Zhang et al., 2015). It is known that AsV is the dominant species in *P. vittata* rhizosphere (Singh and Ma, 2006). In a hydroponic study, Mathews et al. (2010) observed that 0.27 mM...
AsIII was oxidized within 8 d with no AsV being reduced. They attributed the AsIII oxidation to AsIII-oxidizing bacteria because no AsIII oxidation was observed under sterile condition. This was supported by Wang et al. (2012) who also detected AsIII oxidation in the growth media and isolated four As-resistant bacteria, one of which was an AsIII-oxidizer. Other studies also isolated several As-resistant bacteria from the rhizosphere of *P. vittata* (Ghosh et al., 2011; Huang et al., 2010). However, though AsIII oxidation is predominant in aerobic soils, most cultured bacteria identified so far are AsV reducers. For example, Ghosh et al. (2011) showed that As-containing LB medium inoculated with As-resistant bacteria had higher levels of AsV reduction (up to 82 mg kg⁻¹) than AsIII oxidation (<5 mg kg⁻¹), suggesting the dominance of As-reducing bacteria in cultivable microbes. This also indicates that most AsIII-oxidizing bacteria have not been cultured successfully and their community structure needs to be identified by culture-independent methods.

To investigate the microbial community of *P. vittata*, Han et al. (2017) analyzed *aroA*-like and *arsC* genes from its rhizosphere soils by using quantitative polymerase chain reaction (qPCR). They found that the gene copies of *aroA*-like were up to 50-fold of that of *arsC*. However, most bacteria with *aroA*-like genes belong to unculturable groups (Han et al., 2017). In *P. vittata* rhizosphere, AsIII oxidation can be important for As hyperaccumulation, as the fern is more efficient in taking up AsV than AsIII (Huang et al., 2011b). For example, Han et al. (2016a) found that *P. vittata* inoculated with an AsIII-oxidizer exhibited higher AsV uptake than that with AsV-reducers. Under anaerobic conditions, AsIII can also be transformed to methylated As species including MMA, DMA and trimethylarsinoxide (TMAO) (Lomax et al., 2012; Jia et al., 2013). The roles of bacteria-mediated As methylation in rice rhizosphere and its contribution to methylated As species in plant tissues have been reported (Zhao et al., 2013a, 2013b). However, since As methylation is more likely occurs under anaerobic conditions, only small amounts of methylated As has been detected in *P. vittata* tissues, indicating As methylation may not be important in *P. vittata* rhizosphere (Kertulis et al., 2005).

3. Arsenic uptake by *P. vittata*

3.1. Arsenate uptake

Plants take up AsV via P transporters (Phr; Table 1) (Ali et al., 2009). As such, P starvation often up-regulates the expression of
P transporters in plants, thus enhancing AsV uptake, while the presence of P inhibits AsV uptake (Muchhal et al., 1996). Conversely, AsV treatment also decreases P assimilation by plants (Clark et al., 2000). In *P. vittata*, the interactions of AsV and P on their uptake has also been investigated. In hydroponic experiments, increasing P supply decreases AsV uptake by *P. vittata*, whereas P starvation increases AsV influx (Fu et al., 2017; Tu and Ma, 2003). Though AsV and P compete for P transporters, As uptake increased in *P. vittata* when agar media were amended with P (Han et al., 2016a). Other studies also reported a positive correlation between As content in different plants in different experimental conditions are not comparable. It is noted that the K_m for AsV uptake in *P. vittata* (0.52–1.1 µM) (Wang et al., 2002) is much lower than other plants including rice (~6.0 µM) (Abdel et al., 2002), *Holcus lanatus* (4.7 mM) (Meharg and Macnair, 1992), *Deschitopsis cespitosa* (4.8–8.3 mM) and *Agrostis capillaries* (1.6–7.3 mM) (Meharg and Macnair, 1991), consistent with its highly efficient As phytoextraction from soils. Based on a radiotracer 32P uptake study, the K_m in *P. vittata* was lower than that in a non-hyperaccumulating fern *Nephrolepis exaltata*, indicating a high affinity for a substrate and a low K_m value indicates a high affinity. Though kinetic parameters obtained from different plants in different experimental conditions are not comparable, it is noted that the K_m for AsV uptake in *P. vittata* (0.52–1.1 µM) (Wang et al., 2002) is much lower than other plants including rice (~6.0 µM) (Abdel et al., 2002), *Holcus lanatus* (4.7 mM) (Meharg and Macnair, 1992), *Deschitopsis cespitosa* (4.8–8.3 mM) and *Agrostis capillaries* (1.6–7.3 mM) (Meharg and Macnair, 1991), consistent with its highly efficient As phytoextraction from soils. Based on a radiotracer 32P uptake study, the K_m in *P. vittata* was lower than that in a non-hyperaccumulating fern *Nephrolepis exaltata*, supporting that *P. vittata* is efficient in taking up AsV (Poynton et al., 2004).

Although P transporters are hypothesized to take up AsV in *P. vittata*, the transporters involved are still unknown (Fig. 2). Recently, DiTusa et al. (2016) identified three P transporters in Phl1 family from *P. vittata* and studied PvPht1; 3 (Table 1). Yeast growth assays show that cells expressing PvPht1; 3 are more sensitive to AsV and accumulate significantly more As than cells expressing AtPht1; 5. Moreover, 32P uptake assays with and without AsV also suggest that PvPht1; 3 has similar affinity for P and AsV and may be responsible for efficient AsV uptake by *P. vittata* (DiTusa et al., 2016). Though PvPht1; 3 is well characterized in yeast, its function in *P. vittata* has not been well elucidated and should be investigated. Besides, other P transporters should also be investigated to further clarify the mechanisms of efficient AsV uptake in *P. vittata*.

3.2. Arsenite uptake

Arsenate is predominant in aerobic soils where *P. vittata* grows (Han et al., 2016b; Xu et al., 2014). However, AsIII may also exist in plant rhizosphere, probably resulting from biochemical transformation by plant roots and AsV reduction mediated by microbes (Figs. 1 and 2) (Han et al., 2017; Moreno-Jiménez et al., 2012). *P. vittata* is less efficient in taking up AsIII than AsV (Wang et al., 2002). It is reported that the V_max of AsIII uptake (V_max = 125–175 nmol g⁻¹ fw) by *P. vittata* is comparable to AsV uptake (V_max = 97–132 nmol g⁻¹ fw), but its K_m at 78 µM is higher than that of AsV at 0.52–1.1 µM, suggesting that *P. vittata* is less efficient in taking up AsIII (Wang et al., 2011). This explains why *P. vittata* accumulates less As under AsIII exposure than under AsV exposure (Huang et al., 2011b).

Unlike AsV, microbes and plants take up AsIII through aquaporins (AQPs), also called major intrinsic proteins (MIPs) (Ali et al., 2009; Chen et al., 2017). In higher plants, MIPs can be classified into seven subgroups, including nodulin-26 like intrinsic proteins (NIPs), plasma membrane intrinsic proteins (PIPs), and tonoplast
As an analogue of silicic acid, AsIII is taken up by rice mainly through the Si transport system, contributing to As accumulation in the grains (Ma et al., 2008). As a result, Si fertilization is effective in decreasing As accumulation in rice. However, in P. vittata, addition of 0.5 mM silicic acid has little effect on its AsIII uptake in a hydroponic system (Wang et al., 2010), indicating that its AsIII uptake system may be different from that in other plants. Other AsIII analogues, like glycerol and antimonite (SbIII), also show little impact on AsIII uptake and root-to-shoot translocation (Xu et al., 2015). In rice, NIPs also mediate AsIII transport and play an important role in regulating As accumulation (Ma et al., 2008). Though most MIPs that mediate AsIII transport are NIPs, some MIPs may also mediate AsIII transport in plants (Mosa et al., 2012).

As a TIP subfamily AQP from P. vittata, PvTIP4;1, was identified and characterized by He et al. (2015). Differential expression patterns were observed for PvTIP4;1 in P. vittata leaf blades and roots in response to AsV exposure. The expression pattern also differs from that of AtTIP4;1 (Yang et al., 2017). Furthermore, PvTIP4;1 expression was also induced by AsIII exposure (He et al., 2015). These results suggest that PvTIP4;1 may be involved in the regulation of AsIII transport in P. vittata.

### 4.3. Arsenate detoxification in P. vittata

#### 4.3.1. Arsenate reduction in P. vittata

Arsenate reduction is a critical step for AsV detoxification in organisms. In microbes, once taken up, AsV can be rapidly reduced to AsIII in cells, followed by efficient efflux to the external environment or sequestration into vacuoles (Bhattacharjee and Rosen, 2007). As a critical detoxification step, AsV reduction is a conserved mechanism from bacteria to plants, including P. vittata (Ellis et al., 2006).

Upon AsV exposure, AsV and AsIII are the main species in the roots and fronds of P. vittata (Ma et al., 2001), showing efficient AsV reduction to AsIII in the rhizomes. The proportion of AsIII in the fronds is greater (50–90%) than that in the roots (10–40%) (Lombi et al., 2002; Pickering et al., 2006; Zhang et al., 2002). Besides, AsV redox activity is detected in the root extract of P. vittata (Duan et al., 2005). When AsV is supplied to P. vittata, As is transported in the xylem sap predominantly as AsIII (93–98%) (Su et al., 2008). Reduction of AsV to AsIII in the roots and efficient loading of AsIII to intrinsic proteins (TIPs) (Amodeo et al., 2002; Chaumont et al., 2001; Danielson and Johanson, 2008). Among them, NIPs are the structural and functional equivalents of the microbial AQPs that mediate AsIII uptake (Zhao et al., 2010a). In A. thaliana, NIP1;1, NIP1;2, NIP5;1, and NIP7;1 are permeable to AsIII and knockout of these genes reduces plant As uptake (Bienert et al., 2008; Isayenkov and Maathuis, 2008; Kamiya et al., 2009). Besides, Arabidopsis NIP3;1 also mediates AsIII transport and plays an important role in AsIII uptake and root-to-shoot translocation (Xu et al., 2015). In rice, OsNIP2;1 functions as an AsIII channel responsible for AsIII uptake and root-to-shoot translocation (Xu et al., 2015). Meanwhile, OsNIP3;1 also mediates AsIII transport and plays an important role in AsIII uptake and root-to-shoot translocation (Xu et al., 2015). In Arabidopsis, NIP3;1 also mediates AsIII transport and plays an important role in AsIII uptake and root-to-shoot translocation (Xu et al., 2015).

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the xylem contribute to its higher proportion of AsIII in the fronds than the roots (Su et al., 2008). However, in those studies, they didn't separate the roots from the rhizomes. Based on Mathews et al. (2010), AsV reduction mainly occurs in the rhizomes. In addition, AsV reduction may also occur in the fronds, as AsIII is present in excised P. vittata fronds exposed to AsV (Tu et al., 2004c).

In microbes, ACR2 (Arsenic Compounds Resistance 2) mediates AsV reduction to AsIII (Bhattacharjee and Rosen, 2007). Homologues of microbial ACR2 are also found in Arabidopsis (Dhanakher et al., 2006; Nahar et al., 2012), rice (Duan et al., 2007), H. lanatus (Bleeker et al., 2006) and P. vittata (Ellis et al., 2006). Previous reports show that plant ACR2, including AtACR2 (AtCDC25) in Arabidopsis, OsACR2 in rice and HlACR2 in H. lanatus functions as an AsV reductase (Table 1) (Bleeker et al., 2006; Dhanakher et al., 2006). The AsV reductase of P. vittata, PvACR2, is similar to other plant ACR2s and can function as AsV reductase in yeast lacking ScACR2, thereby enhancing AsV tolerance and decreasing As accumulation in yeast cells (Ellis et al., 2006). Moreover, PvACR2 is unique due to its lack of phosphatase activity and its constitutive expression, which may play an important role in As-hyperaccumulation in P. vittata. In addition, P. vittata may also express other AsV reductases, like PvVZS-8, which correspond to a “predicted protein sequence of a putative AsV reductase” (Cesato et al., 2015).

Though PvACR2 is critical for As metabolisms in P. vittata, recent evidence shows that canonical ACR2 probably does not confer AsV reduction in plants (Liu et al., 2012). Instead, a new category of AsV reductase ARQ1 (Arsenate Reductase QTL1)/HAC1 (High Arsenic Content 1), different from ACR2, is critical for AsV reduction, tolerance and As accumulation in Arabidopsis and rice (Sánchez-Bermejo et al., 2014). However, whether functional ARQ1/HAC1 exists in P. vittata is unclear.

Besides ACR2, glutaredoxin (Grx) may also play a role in AsV reduction and regulate the cellular AsII levels, though the mechanistic details for its function are yet to be resolved (Sundaram et al., 2008). PvGrx5, a GSH-dependent oxidoreductase from P. vittata, decreases As accumulation in the leaves in transgenic Arabidopsis (Table 1) (Sundaram et al., 2009). In addition, several enzymes including triose phosphate isomerase (TPI) (Rathinasabapathi et al., 2006) and glyceraldehyde-3-phosphate dehydrogenase (Bona et al., 2010, 2011) may also be involved in AsV reduction in P. vittata (Table 1). It is also possible that AsV is reduced non-enzymatically by GSH, which is oxidized to oxidized GSH and recycled by GSH reductase (Singh et al., 2006). Taken together, AsV reduction in P. vittata is important for its As detoxification. Future studies need to identify enzymes that participate in this process, together with their tissue specificity and efficiency.

4.2. Arsenite translocation to the fronds

After being taken up, most AsV is reduced to AsIII in the rhizomes, with both AsV and AsIII being transported to the shoots via xylem loading (Fig. 2). In non-hyperaccumulators, only small amounts of the root As is translocated to the shoots (e.g., ~2.6% in A. thaliana), and a considerable amount of As is complexed with phytocelatins (PCs) and transported into root vacuoles by ATP binding cassette subfamily C1 (ABCC) transporters (Table 1) (Song et al., 2010, 2014). In P. vittata, thios including PCs and GSH have been examined, but only a small part (1–3%) of the As can be complexed with PCs (Zhao et al., 2003). Moreover, large amounts of As are translocated to the fronds, mainly as AsIII (Lessl et al., 2015; Lombi et al., 2002; Tu and Ma, 2007). The data suggest that in P. vittata, As detoxification is independent of PCs. Instead, As detoxification is associated with rapid reduction of AsV to AsIII in the rhizomes and efficient AsIII translocation to the fronds.

In most plants, AsIII is the main form being loaded into the xylem (Zhao et al., 2009). For rice, AsIII transport to xylem is via the Si transporter Lsi2 (homologue of ArsB in E. coli) (Table 1) (Yamaji and Ma, 2011). Compared to non-hyperaccumulators, little is known about the transporters responsible for AsIII translocation in P. vittata (Fig. 2).

4.3. Arsenite efflux to the external environment

To date, many plants including A. thaliana, H. lanatus, Trifolium aestivum, Hordeum vulgare, Zea mays and rice are known to efflux AsIII to the external medium (Xu et al., 2007; Zhao et al., 2009). In rice, AsIII influx transporter Lsi1 also mediates AsIII efflux (Zhao et al., 2010b). However, this pathway only accounts for 15–20% of the total AsIII efflux in rice, indicating the existence of other efflux transporters.

Unlike typical plants, P. vittata shows little AsIII efflux (Huang et al., 2011b; Su et al., 2008). When exposing to <1.5 mg l\(^{-1}\) AsV for 24 h, AsIII efflux in P. vittata roots is much lower (≤2 μg g\(^{-1}\) root fw) than that in other plants, such as tomato and rice (>60 μg g\(^{-1}\) root fw) (Huang et al., 2011b). Su et al. (2008) concluded that limited AsIII chelation and efflux in the roots, and efficient AsIII xylem loading contributed to As hyperaccumulation in P. vittata. Since little AsIII efflux occurs in P. vittata roots, this process is not considered critical for As detoxification in P. vittata. However, recent studies showed that under sterile condition with high As exposure, significant AsIII efflux occurs in P. vittata roots, which may play a role in As detoxification under high As stress (Chen et al., 2016; Han et al., 2016a). To date, the associated molecular mechanisms of AsIII efflux in plants are unclear, including P. vittata (Fig. 2).

4.4. Arsenite sequestration into vacuoles

Arsenite sequestration into vacuoles in the fronds is critical for As storage, detoxification and hyperaccumulation in P. vittata (Lombi et al., 2002; Pickering et al., 2006). Indriolo et al. (2010) isolated two P. vittata ACR genes, ACR3 and ACR3:1, encoding proteins similar to yeast ACR3 (Table 1). As an AsII efflux transporter, PvACR3 localizes on the vacuolar membrane and confers AsIII sequestration into vacuoles in P. vittata fronds (Indriolo et al., 2010). However, Chen et al. (2013) showed that PvACR3 localized on the plasma membrane in transgenic Arabidopsis, which mediated AsIII efflux and its xylem loading in Arabidopsis roots. In brief, P. vittata ACR3s play critical roles in AsIII sequestration in the fronds and the function of different ACR3s should be investigated in future.

5. Concluding remarks

Much research has been devoted to understand the mechanisms of As metabolisms in P. vittata. In soils, root exudates and rhizobacteria activities play important roles in As solubilization and transformation. However, unlike other plants that extrude oxalate and citrate, P. vittata produces phyteate in the root exudates (Fu et al., 2017; Liu et al., 2016; Lessl and Ma, 2013; Tu et al., 2004a). So phyteate is special to P. vittata, which may contribute to its efficient solubilization of Fe, Ca, P and As in the rhizosphere soils (Fig. 1).

In addition, microbes-mediated As transformation in P. vittata rhizosphere is also important (Fig. 1). As reported by Han et al. (2016a), AsIII efflux to the external environment occurs in P. vittata roots where AsIII is then oxidized to AsV by bacteria, allowing more efficient As uptake as P. vittata is more efficient in taking up AsV than AsIII (Huang et al., 2011b). Thus, efficient As uptake by P. vittata is mediated by microbial As transformation. Since most studied rhizobacteria of P. vittata belong to AsV reducers (Ghosh et al., 2015a; Huang et al., 2010; Wang et al., 2012) and araA
like and escG genes can not be fully amplified based on the reported primers (Escudero et al., 2013; Han et al., 2017), further studies should pay more attention to the behaviors and biodiversity of functional genes of As(III) oxidizers and As(V) reducers. Since P. vittata displays staggering efficiency in As accumulation, high-affinity P transporters for As(V) uptake, efficient As(III) reductase, xylem loading transporters, and As(III) sequestration transporters are all involved. Though some critical genes have been discovered in P. vittata, more critical genes should be identified and characterized, which may be used to increase As uptake and accumulation in plants for phytoremediation. Taken together, P. vittata has evolved mechanisms for efficient As solubilization in rhizosphere soils and effective As uptake, translocation and detoxification in plants. Further studies are needed to better understand the As hyperaccumulation mechanisms in P. vittata, which can expand our knowledge on plant As metabolism and also improve phytoremediation of As-contaminated soils using P. vittata.

Acknowledgements

This work was supported in part by Key Project of Natural Science Foundation of China (21637002), Jiangsu Provincial Natural Science Foundation of China (No. BK20160649), the National Key Research and Development Program of China (Grant No. 2016YFD080001), the Research Fund for the Doctoral Program of Higher Education of the State Education Ministry (No. 20130091110027) and Program B for Outstanding Ph.D. Candidates of Nanjing University (No. 2016010801).

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