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Accepted Version

Anawar, H. M., Rengel, Z., Damon, P. and Tibbett, M. ORCID: https://orcid.org/0000-0003-0143-2190 (2018) Arsenic-phosphorus interactions in the soil-plant-microbe system: dynamics of uptake, suppression and toxicity to plants. Environmental Pollution, 233. pp. 1003-1012. ISSN 0269-7491 doi: https://doi.org/10.1016/j.envpol.2017.09.098 Available at https://centaur.reading.ac.uk/73306/

Publisher: Elsevier

Arsenic-phosphorus interactions in the soil-plant-microbe system: dynamics of uptake, suppression and toxicity to plants

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ABSTRACT

High arsenic (As) concentrations in the soil, water and plant systems can pose a direct health risk to humans and ecosystems. Phosphate (Pi) ions strongly influence As availability in soil, its uptake and toxicity to plants. Better understanding of As(V)-Pi interactions in soils and plants will facilitate a potential remediation strategy for As contaminated soils, reducing As uptake by crop plants and toxicity to human populations via manipulation of soil Pi content. However, the As(V)-Pi interactions in soil-plant systems are complex, leading to contradictory findings among different studies. Therefore, this review investigates the role of soil type, soil properties, minerals, Pi levels in soil and plant, Pi transporters, mycorrhizal association and microbial activities on As-Pi interactions in soils and hydroponics, and uptake by plants, elucidate the key mechanisms, identify key knowledge gaps and recommend new research directions. Although Pi suppresses As uptake by plants in hydroponic systems, in soils it could either increase or decrease As availability and toxicity to plants depending on the soil types, properties and charge characteristics. In soil, As(V) availability is typically increased by the addition of Pi. At the root surface, the Pi transport system has high affinity for Pi over As(V). However, Pi concentration in plant influences the As transport from roots to shoots. Mycorrhizal association may reduce As uptake via a physiological shift to the mycorrhizal uptake pathway, which has a greater affinity for Pi over As(V) than the root epidermal uptake pathway.

Capsule: *Understanding As-Pi interactions in the soil-plant systems can help in reducing the As uptake by crop plants and protecting the food chain.*

Keywords: Arsenic toxicity. As-Pi interactions. As-Pi uptake by plants. Soil mineralogy. Soil types. Mycorrhizal association

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1. Introduction

1.1. Arsenic in the environment

Arsenic is generally considered one of the top priority elements for carcinogenicity and toxicity to humans, animals and plants (ATSDR, 2007). Several severe incidents of As poisoning have occurred in regions such as Bangladesh, India (West Bengal) (Anawar et al., 2002), Vietnam, Taiwan and northwest China (Wang et al., 2002). Sources of high contents of As in the environment are either geogenic in groundwater aquifers (Salmon et al., 2014) or anthropogenic, typically associated with mining, industrial waste and agricultural chemicals (Anawar et al., 2011). Average concentration of As in the Earth's crust is 1.5 μg/g with the median value of 6.0 μg As /g for uncontaminated soils (Bowen, 1979). The average As contents in agricultural fields that received As-containing pesticides and defoliants range from 5-2553 mg/kg (Walsh and Kenny, 1975). Early mining and smelting operations led to contamination of the agricultural land, with soil As levels of 539-9380 mg/kg in Korea (Jung et al., 2002), 11.1-651.1 mg/kg in Portugal (Pratas et al., 2005), etc. The As concentration in human hair exhibits significant relationship with that in rice (*Oryza sativa L.*), wheat (*Triticum aestivum* L.) and agricultural soils (Rahman et al., 2007, 2008) in As-affected areas reflecting human exposure to As via the soil–plant transfer pathways (Geng et al., 2006; Huang et al., 2006). These studies indicate widespread occurrence of As, and its contamination effects on agricultural soils.

1.2. As-Pi chemistry and their competition

Under aerobic conditions, As and phosphorus (Pi) form stable tetrahedral oxyanions (As(V) and orthophosphate, Pi) of $^{+}5$ oxidation state due to similar chemical characteristics (Manning and Goldberg, 1996; Lambkin and Alloway, 2003). In soil, As predominantly exists in the inorganic forms (arsenate, As(V) and arsenite, As(III)) with minor concentration of dimethylarsinic acid (DMAA) and monomethylarsenic acid (MMAA) (Pantsar-Kallio and Manninen, 1997; Quaghebeur et al., 2003; Quaghebeur and Rengel, 2005). Because of their physico-chemical similarity, As(V) and Pi ions interact strongly competing for the same charged surfaces in soil. Arsenate uptake by plants occurs via the similar carrier process as Pi (Pickering et al., 2000; Zhao et al., 2009) with Pi having more affinity for transport sites than As(V) (Ullrich-Eberius et al., 1989; Meharg et al., 1994; Dunlop et al., 1997). For plant growth, Pi is an essential macronutrient. The nucleic acids, phospholipids and ATP contain Pi, that is involved in regulating key enzyme reactions and metabolic pathways (Schachtman et al., 1998; Rose et al., 2013).

1.3. As-Pi interactions and significance of this review

A lot of research works have studied the As-Pi interactions in the environment with conflicting results (Vetterlein et al., 2007; Zhao et al., 2009; Szegedi et al., 2010). On one hand, Pi can decrease plant As uptake, and on the other hand, it may promote the availability of As in soil and increase plant uptake. Therefore, it is necessary to explore the mechanism of action between As and Pi under different environmental conditions. Most studies, to-date, have failed to account for the complexity of interactions between Pi and As in soil-plant system, and the variability in competition between As and Pi depending on soil types and substrate conditions. Furthermore, the mechanisms of how Pi, when used as fertilizer, ameliorate As toxicity to crop plants (Peryea, 1998) are not yet clear (Geng et al., 2005). Although the major factors have been identified, the net effect of their interactions is poorly understood. Therefore, further research is essential to assess the available knowledge, identify the research gaps for the future work, understand the As-Pi interactions in soil-plant systems, and their effects on exacerbation and/or amelioration of As toxicity, because these results can help to decrease the risk of As toxicity to plants, animals and humans. Therefore, this study reviewed (1) As-Pi interactions in soil-plant continuum, (2) the effect of soil type, soil properties and minerals on As-Pi interaction in soils, (3) the role of different Pi transporters in Pi and As uptake by plants, (4) the mechanisms of As and Pi uptake in As-tolerant and As-intolerant plants, (5) how mycorrhizal symbioses and bacteria influence As and Pi uptake by plants and As toxicity, and (6) case studies of As and Pi uptake by As-tolerant and As-intolerant genotypes, and P-deficient and P-sufficient plants. This review investigates the role of Pi on As uptake and toxicity to plants, elucidate the key mechanisms and factors affecting the As : Pi interactions in soils and plants, identify key knowledge gaps and recommend new research directions.

2. Influence of soil property, mineralogy and soil types on As and Pi sorption to soils

Due to a smaller size and higher charge, Pi anions bind to soil more strongly and higher than As(V) (Lambkin and Alloway, 2003) at similar Pi and As concentrations (Woolson et al.,

1973) making more As available by plant uptake (Zou et al., 2009). Due to slow sorption to soil, Pi become more competitive than As(V) over time (Lambkin and Alloway, 2003). According to the Steindorf-Rebhun-Sheintuch equation, ligand exchange theory and a share charge hypothesis, Pi has more probability to replace As(V) from soils (Roy et al., 1986; McBride, 1994). However, Pi could also be desorbed by As due to a mass action effect of high As:Pi concentrations in soil solution (Lambkin and Alloway, 2003). The fast adsorption of As and Pi occurred by exchange adsorption, while slow adsorption by specific adsorption in the acid, neutral and calcareous purple soils (Zou et al., 2009).

The soil mineralogy, soil texture, soil properties and environmental factors that may greatly affect the As-Pi interaction, mobility and availability of As in soils (Bissen and Frimmel, 2003) and uptake by plants include mineral components, presence of anions (e.g., citrate, phosphate, phytates/phytic acid (Dalal, 1977; Marschner, 1995), residence time, pH, redox potential, organic matter (OM), microbial activity and especially, Fe- and Al-oxide/ hydroxides (Melamed et al., 1995; Turpeinen et al., 1999; Fitz and Wenzel, 2002; Kubicki, 2005). Among these factors, goethite and pH strongly control the behaviour of As and Pi. Knowledge of As(V) adsorption on individual soil minerals may predict As(V) adsorption in whole soils and its response to Pi addition (Manning and Goldberg, 1996). Fordham and Norrish (1979) and Violante and Pigna (2002) found that Fe and Mn-rich minerals such as goethite, nontronite, ferruginous smectites, birnessite and pyrolusite absorbed more As(V) than Pi when supplied in equal molar ratio, but more Pi than As(V) was sorbed on noncrystalline Al containing minerals e.g., gibbsite, boehmite, allophane and clay fractions (e.g., kaolinite, illite and vermiculite) resulting in higher As(V) desorption and uptake by Indian mustard (*Brassica juncea* L.) (Bolan et al., 2013). A high rate of goethite addition to soils can reduce Pi and As uptake by plants (Vetterlein et al., 2007). The Pi and Fe addition to high As soils using a sequential incorporation method can significantly decrease As toxicity to lettuce root growth by supplying a nutrient source (Koo et al., 2013).

In case of sandy soils/sandy loam, Pi addition displaced As(V) ions from the surface of sand grains due to a low number of sorption sites and increased As uptake by plants, thus decreasing plant growth (O'Neill, 1992; Woolson et al., 1973), but increased vegetative yields of wheat, barley, sudangrass and lucerne (Creger and Peryea, 1994) decreasing As uptake and toxicity on a silty clay loam (Woolson et al., 1973), a silty loam (Jacobs and Keeney, 1970) and clay loam and sandy clay loam soils (Pigna et al., 2010). Arsenic mobility and solubility in anion-fixing soils or alkaline soils can be strongly affected in case of high P supply (Smith et al., 1998; Violante and Pigna, 2002). As(V) and Pi adsorption-desorption had the similar characteristics and followed the Langmuir and Freundlich equations in the low pH (acid), neutral and high pH soils (calcareous purple soils) (Zou et al., 2009), but they are not always dependent on each other due to dissolution and mobility of un-reactive P at low pH (Mwamila and Gustafsson, 2011).

3. As-Pi interaction, uptake and arsenic toxicity in plants

3.1. Mechanisms of As toxicity to plants

The predominant effect of As toxicity in the cell is oxidative stress (Finnegan and Chen, 2012) that reduces seed germination, root and shoot growth and root surface area, etc. (Smith et al., 2010), restrict nutrients and water uptake, and cause nutrient deficiency in plants (Paivoke and Simola, 2001). After reduction arsenic (As(III) forms chemical bond with sulphydryl groups and deactivates some enzymes (Delnomdedieu et al., 1993), and increases reactive oxygen species and lipid peroxidation, but decreases the superoxide dismutase activity and antioxidants levels (Raab et al., 2004) resulting in cellular membrane damage (Mascher et al., 2002; Tuan et al., 2008). In contrast, Pi supply to As-treated plants decreased activities of CAT, APX and lipid peroxidation, and thus decreased membrane damage (Gunes et al., 2009). Arsenate in the cytoplasm competes with Pi forming unstable ADP-As(V), and disrupt the energy flows in cells (Hartley-Whitaker et al., 2001, 2002). High S concentrations in soil (e.g., via micronutrient fertilizers) alleviated the toxicity effect of As on plant growth although Pi addition to soil enhanced As uptake by plants (Grifoni et al., 2015). This phenomenon occurred due to formation of glutathione and phytochelatins, their chelation with As and subsequent sequestration of these chelated complexes in the vacuoles (Cobbett, 2000; Hartley-Whitaker et al., 2001). Although Pi supply suppressed the As uptake by plants in the hydroponics, high S addition increased As uptake and decreased Pi content influencing the As-Pi interaction in plants. Application of As and Zn to soils shows an antagonistic relationship such as Zn in soils (at application rate of 3 mg/L) reduced As availability in soils and uptake in plants (Sanchary and Huq, 2017). Arsenic accumulation by plants is controlled by the oxidation state, As and P forms and plant species.

Arsenic hyperaccumulator plant species (e,g,, *Pteris vittata*) detoxify As toxicity in a number of ways such as transformation of As(V) to As(III) by enzyme and compartmentalization in subcell; capturing reactive oxygen species by phytochelatin and thiols, preventing lipid peroxidation (Shoji et al., 2008; Bona et al., 2011) and maintaining a greater ratio of P/As in the roots, at least 1.2 in soil solution or 1.0 in fronds (Tu and Ma, 2003a; Singh and Ma, 2006). Therefore, Pi application may be an important strategy for As detoxification, enhanced growth of *Pteris vittata* and efficient As uptake to phytoremediate As-contaminated soils (Kertulis et al., 2005; Ye et al., 2011; Yan et al., 2012). The in-situ measurement of As/Pi molar concentration ratio can predict As phytotoxicity, where As/Pi ratio of 0.168–0.360 resulted in a 50% reduction of wheat (*Triticum aestivum*) growth (Mojsilovic et al., 2011).

3.2. As-Pi interactions and uptake by plants grown in soils

The competition between As and Pi, and the effect on their uptake by plants grown in soils are described briefly in Table 1. Arsenate uptake from soil occurs via the same transport system as Pi (Pickering et al., 2000), however, the effects of As on plant metabolism are complex and only partially understood. An application of Pi had variable effects on the sorption and mobility of As in soils, uptake by plants and toxicity effects with both increases (Lambkin and Alloway, 2003; for 10 mg P/ kg in Geng et al., 2005; 238.4-423.2 mg As/kg soil and 10.0 mM phosphate addition in Tao et al., 2006) and decreases (Hanada et al., 1975; for 40 mg P/ kg in Geng et al., 2005; Pigna et al., 2012) reported. Nevertheless, increasing Pi concentration could not resist a fraction of 'steady state' As(V) uptake, while As(V), in contrast, can inhibit 'steady state' Pi uptake mildly (Geng et al., 2005). Therefore, the interaction of As and Pi, and suppressive effect of one on another is not straight forward. It is not yet studied how As interacts with organic P in soil. Irrigating As-rich water may change the As-Pi balance in soil solution, causing mobilisation of Pi and subsequent losses by leaching or higher Pi availability for plant nutrition. But higher As toxicity can affect crop yields as well (Talukder et al., 2011, 2012). The mobility of As and Pi, and As toxicity decreases due to formation of recalcitrant forms in aged soil (Onken and Adriano, 1997; Lombi et al., 1999).

The soil Pi status was related to As uptake by *Urtica dioica*, but not by *Phragmites australis* indicating a differential response of plants to Pi (Ahmed et al., 2011). The uptake kinetics of As and Pi by different plant species over short or long time vary depending on the genus and species of plants. Therefore, further research is necessary to understand a time-course of Pi and As(V) uptake by different plant species. Compared to non-tolerant *Holcus lanatus*, the tolerant clones generally contained a higher proportion of As(V) (Quaghebeur and Rengel, 2003). Arsenic uptake by and growth of rice cutgrass (*Leersia oryzoides* Sw.) and tall fescue (*Festuca arundinacea* Schreb.) was not enhanced by P fertilization above a minimal amount (Klaber and Barker, 2014). The application of Fe^{2+} to the rice fields under flooded and reduced condition decreased the As uptake in rice grain and increased their yield, while Pi application demonstrated the opposite results (Hossain et al., 2009).

3.3. Impact of Pi availability on As uptake by plants in hydroponics

Phosphate and As(V) interactions in hydroponics and plant accumulation are largely investigated (Khattak et al., 1991; Clark et al., 2000; Pickering et al., 2000; Esteban et al., 2003; Panuccio et al., 2012; Shaibur et al., 2013) and briefly summarized in Table 2 and Fig. 1. Most studies found that Pi deficiency in nutrient solutions increased the capacity of rice and *Lemma gibba* plants to take up more Pi and As(V), but at low As concentration, high Pi treatment decreased As(V) uptake and toxicity (Macnair and Cumbes, 1987; Mkandawire et al., 2004; Lihong and Guilan, 2009; Panuccio et al., 2012) via suppression of the high-affinity Pi/As(V) transport system. The supply of Pi also influenced the As speciation and transport (Lei et al., 2012). The *Isatis cappadocica*, a robust perennial rosette plant, can grow in highly impacted As-contaminated areas and hyperaccumulates As in its areal parts in hydroponic media (Karimi and Souri, 2015).

Phosphate can suppress As(V) uptake in phytoplankton (Planas and Healey, 1978), *Oryza sativa* (Abedin et al., 2002), *Lupinus albus* (Esteban et al., 2003), barley (Shaibur et al., 2013) and As-tolerant species such as *Holcus lanatus, Cytisus striatus* (Meharg and MacNair, 1992; Bleeker et al., 2003) and *Pteris vittata* (Wang et al., 2002; Tu and Ma, 2003b) grown in hydroponic systems. The time-dependent split-Pi application (P_{134+66} and P_{66+134}) with low initial Pi application increased the growth of *Pteris vittata* L. and the efficiency of As removal, that was higher than high initial Pi-supply (P_{200+0}) (Santos et al., 2008). The radial loss of O_2 from aerenchyma structures converts the rice root surface into much more highly oxidized condition compared to the surrounding environment (Colmer, 2003) and forms Fe-oxide plaques on the root surface (Taylor et al., 1984).

The As-Pi interactions and their uptake by plants produced different and often contradictory results depending on soil substrates and hydroponic conditions. The kinetics of Pi and As accumulation in plants in hydroponics is overestimated compared to soil experiments, because some processes such as water flow, redox potential, diffusion, adsorption/desorption and ion exchange by minerals (Fe, Mn and Al oxyhydroxides, clay minerals, sulfide minerals, etc.) and organic components are common in soil systems that control As and Pi solubility and mobility in soils (Bissen and Frimmel, 2003; Anawar et al., 2008), while these processes do not occur in hydroponics (Fitz and Wenzel, 2002). Hence, the results from the hydroponic experiments can not be extrapolated to and may have limited validity for soil-grown plants (Fitz and Wenzel, 2002). However, the hydroponics studies can provide new knowledge on the membrane transport.

3.4. Relation of plant P status with As uptake

Quaghebeur and Rengel (2004) showed that P level in plant and As-Pi interactions in soil are pivotal factors controlling As and P uptake by plants. The Pi deficiency can enhance As uptake by plants e.g., *Pteris vittata* (Lei et al., 2012), P-deficient canola (Quaghebeur and Rengel, 2004) and white lupin (*Lupinus albus*) (Esteban et al., 2003), causing a decline in plant growth (Wang et al., 2002; Geng et al., 2006) except *Pteris vittata*. The low As uptake and amelioration of As(V) toxicity in most of the +P plants occurs by competition with Pi except lupin (Esteban et al., 2003; Reina et al., 2005). The P-deficient white lupin plants develop proteoid roots and take up more Pi and As(V) (Esteban et al., 2003; Reina et al., 2005), but lower translocation of As to shoot compared to corn plants (Vetterlein et al., 2009). The presence of As(V) stimulated P uptake by P-deficient plants and reduced it for the P sufficient ones. However, the concentration of As in rice and barley shoots grown in hydroponics was very lower in P-deficient plants than in P-sufficient ones due to reddish iron plaque formed on the root surface sequestering As and decreasing its uptake by roots (Chen et al., 1980; Liu et al., 2004; Shaibur et al., 2013). Furthermore, it is assumed that high P level in As-tolerant plants could alleviate As toxicity more efficiently than non-tolerant ones, and despite the decreased As(V) uptake, As-tolerant plants might have higher total concentration of As in their biomass over long time (Campos et al., 2014).

Higher molar ratio of Pi/As in rice (*Oryza sativa*) shoots of Indica cultivar than for the hybrid Indica variety (Lu et al., 2010) suggested the genotypic difference in response to As(V) toxicity and potential capacity to breed rice cultivars for As affected paddy soils (Geng et al., 2006).

3.5. High-affinity and low-affinity Pi transporter for Pi and As uptake

The different families of transporter proteins are involved in Pi transport through plant plasma membranes by a highly complex network of regulation, e.g., PHT1 transporters for Pi accumulation from soil (Nussaume et al., 2011). Plants have developed different controlled adaptative mechanisms to acquire necessary amount of external Pi and maintain Pi homeostasis as well as overcome low Pi availability (reviewed in Schachtman et al., 1998; Rouached et al., 2010). In the low Pi environment, Pi and As(V) accumulation by plants are controlled by the Pht1;9 and Pht1;8 membrane transporters through activation of high-affinity Pi transport system (Rausch and Bucher, 2002; Remy et al., 2012). Arsenate inhibited the root growth of non-tolerant *Holcus lanatus* plants more strongly than the tolerant genotypes. The tolerant plants (e.g., *Holcus lanatus*, *Silene vulgaris* and Agrostis species) took up less As(V) than non-tolerant ones over short time (Porter and Peterson, 1977; Zhao et al., 2009) supporting the hypothesis that a suppressed high-affinity Pi transport system provides As resistance together with increased Pi/As ratio and strong selectivity against As(V) (Macnair and Cumbes, 1987). However, total As accumulation is higher in tolerant than non-tolerant plants over long time, as the latter become unhealthy and die relatively quickly (Puckett et al., 2012).

As(V) and Pi compete for transporters across root plasma membrane (Smith et al., 2010). Recently, Panuccio et al. (2012) indicated that As(V) resistance of *Pennisetum clandestinum* Hochst (kikuyu perennial grass) occurs due to enhanced Pi nutrition, and not due to downregulation of the Pi uptake system. Aquaglyceroporins (AQP3, AQP7, AQP9, and AQP10) mediate the bidirectional movement of arsenite across cell membranes (Jung et al., 2012). The As(III) transport was not affected by Pi in rice.

3.6. Effect of root exudates on As and Pi uptake

The plant root exudates play critical roles in As and Pi release from soil matrix. The main factors controlling the mobility of As in surrounding environment of roots and uptake by plants include solubilisation of As from the soil matrix/minerals, very large surface areas of roots (Pollard et al., 2002), rhizosphere pH, and chelating agent (Quaghebeur et al., 2005; Marschner, 1995). The root exudates including organic acids and phenolics released by the P-deficient plants can mobilize Pi and As from soil matrix including Fe-oxides/hydroxides, and enhance availability to plants by changing soil pH and through forming soluble metal-chelate complexes (Hoffland, 1992; Strom et al., 1994; Kirk et al., 1999).

3.7. Does As resistance occur via decreased As uptake or protective effect of high Pi uptake?

Arsenic tolerance in higher plants hinges on decreased As accumulation by suppression of the high-affinity Pi/As(V) uptake system in roots (Meharg and Macnair, 1992) and decreased As transport to shoots (Pigna et al., 2009), both of which are dependent on high shoot Pi status that outcompetes As in metabolic reactions as reported for the *ars1* Arabidopsis mutants (Lee et al., 2003) and vacuolar sequestration of As in shoots. However, our data analysis from Pigna et al. (2009, 2010) and Lewinska and Karczewska (2013) demonstrate the new results as follows: Pi application to soils not only augmented plant growth, but also increased As and Pi concentrations in shoot of wheat (*Triticum durum* L.) irrigated with As-rich water (Fig. 2). Therefore, it is clear that Pi addition to soils alleviated As toxicity not by decreasing As uptake by plants, but increasing the plant biomass, Pi nutrition and metabolic reactions. Joardar and Kawai (2014) and Christophersen et al. (2009a) also reported that the decreased As toxicity occurred not due to lower As uptake by plants, but increased Pi uptake by plant root surface and transport to shoot (Campos et al., 2014). A more detailed investigation of uptake of As(V) and Pi is necessary to clarify this hypothesis. Our recent study indicated that P addition to topsoil (upper 5 cm) of three-layered soil system with As in the subsoil (> 10 cm) was a more effective strategy to impove the plant growth by alleviating As toxicity, increasing P concentration, but reducing As level in plant biomass than P application in subsoil (Anawar et al., 2016).

4. Role of mycorrhiza on As-P interaction in soil system and uptake by plant

The symbiotic association of arbuscular mycorrhizal (AM) fungi with plant roots growing in As-contaminated soil has been demonstrated to improve P nutrition, reduce As(V) uptake, increase P/As ratios in the shoots, and alleviate As toxicity for several plant species (Fig. 3) (Meharg et al., 1994; Chen et al., 2007; Ultra et al., 2007; Xia et al., 2007; Xu et al., 2008; Christophersen et al., 2009b, 2012; Ahmed et al., 2006, 2011). Albeit some studies did not demonstrate good responses to AM fungi for tolerance to soil As (Knudson et al., 2003; Zhu et al., 2003; Li et al., 2006; Grace et al., 2009), indicating that the benefits of the AM association may not be universal for all scenarios (e.g., basin wildrye).

Based on demonstrated studies it is reported that AM plant roots may have physiologically altered Pi uptake systems, whereby there is a switch from the epidermal uptake pathway to an AM uptake pathway following colonisation. Considering the physiological and molecular evidence, Smith et al. (2003) showed that AM plants have two pathways for Pi and As(V) uptake: direct pathway via high-affinity Pi transporters Pht1;1 and Pht1;2 in the epidermis and root hairs in AM and NM (non-mycorrhizal) plants (Schunmann et al., 2004a,b; Shin et al., 2004) regardless of their responsiveness (Smith et al., 2010). The down-regulation of expression of high-affinity Pi-uptake pathway lowered Pi and As(V) uptake in AM barley and genotypes of As-tolerant *Holcus lanatus*, but other studies indicated no such effect (Grace et al., 2009). However, it suggested that the AM and direct Pi uptake pathways are integrated, and Pi and As(V) uptake may be inter-dependent (Smith et al., 2003, 2004; Smith and Read, 2008), although details of the mechanisms are still unclear.

The transporters in external hyphae of the AM fungi in symbiosis condition uptake Pi via the mycorrhizal pathway (Maldonado-Mendoza et al., 2002). The hyphae transports Pi along a long way (Ezawa et al., 2002) and transfer to plant across a symbiotic interface to cortical cells by induction of Pht1;8 in roots (Paszkowski et al., 2002; Glassop et al., 2005). Thus, a higher amount of Pi and exclusion of As are promoted by the AM pathway that protect plants against As uptake and toxicity (Christophersen et al., 2009b). It suggested that AMF decreased As toxicity in soil by converting As speciation from inorganic to organic forms by hyphae-produced glomalin (Ultra Jr et al., 2007; Chern et al., 2007; Smith and Read, 2008) and acting as a barrier for As uptake (Ultra Jr et al., 2007; Ahmed et al., 2011) through several physical mechanisms: adsorption onto plant or fungal cell walls in plant tissues or extra-radical mycelium in soil (Hildebrandt et al., 1999; Kaldorf et al., 1999; Joner et al., 2000); exclusion by precipitation onto polyphosphate granules (Turnau et al., 1993). Some studies reported that lower As uptake in shoot occurred mainly due to a “dilution effect” from increased growth of AM plants and decreased As partitioning to shoots, rather than decreased As uptake per plant (Chen et al., 2007; Zhao et al., 2009; Ahmed et al., 2011). Therefore, further research is needed to determine the effects of AM fungi-induced various metabolic strategies for As resistance mechanism and As uptake by plants. A recent study suggests that mycorrhizal colonization converts As into non-toxic compexes by enhancing the production of cysteine, glutathione, non-protein thiols, and activity of glutathione-S-transferase in plants indicating the multifarious role of AMF in alleviation of As toxicity (Sharma et al., 2017). Furthermore, Pi from superphosphate fertilizer or other sources may suppress the AMF colonization, change the structure of the AMF community (Shetty et al., 1995; Ahmed et al., 2011) and thus strongly influence any potential AM effect on As resistance. Combined application of inoculum and Pi to soil augmented plant biomass, reduced As toxicity and increased plant Pi nutrition; and these effects were higher than inoculation only with native AMF (Cozzolino et al., 2010; Cattani et al., 2015).

Glomus mosseae that was more tolerant and unaffected by the high concentrations of As (e.g., 200 mg/kg) than *Medicago truncatula* plant, increased host plant As tolerance and Pi nutrition (Xu et al., 2008). Not only AMF, but also ericoid and ectomycorrhizal fungi can increase their tolerance to As(V) contamination via different mechanisms (Sharples et al., 1999, 2000a). The ericoid mycorrhizal fungus *Hymenoscyphus ericae* from an As and Cu mine spoil has adapted to As(V) contamination by decreasing As uptake via enhanced As(III) efflux (Sharples et al., 2000b), but the mechanisms behind this process are still unclear. Three species of ectomycorrhizal fungi showed variable response to arsenate toxicity under the influence of PO_4^{3-} concentration (Chen and Tibbett, 2007). The *Suillus variegatus* and *Hebeloma crustuliniforme* exhibited the high sensitivity to As toxicity at low Pi treatments, while the higher Pi treatments reduced As toxicity. In contrast, the *Cenococcum* *geophilum* exhibited higher tolerance to As; and Pi did not show ameliorating effect on As toxicity in *C. geophilum.*

5. Influence of soil microbial communities on As and Pi uptake by plants

Microbial activity causes transformation of As sepcies by reduction (arsenate to arsenite), oxidation (arsenite to arsenate), and methylation (Wang et al., 2004; Qin et al., 2006; Cai et al., 2009). Arsenic reduces the soil functional gene diversity, while Pi increases the soil microbial community structure. The rhizobacteria accelerate As hyperaccumulation by *P. vittata* (Xiong et al., 2010), even under a Pi-limiting environment (e.g., insoluble phosphate rock in alkaline soil) in As-rich media (Lessl and Ma, 2013; Lessl et al., 2014). By excreting acids, protons, and siderophores, the rhizobacteria can cause dissolution of phosphate rock and minerals that improve plant Pi nutrition and As uptake by plants (Duponnois et al., 2005; Ghosh et al., 2015). Due to the continuous excretion of plant released organic substrates, the number of microorganisms in the rhizosphere increases compared to the non-rhizosphere soil resulting in a more diverse bacterial community (Marschner, 1995). Microbial reduction of As(V) to As(III) occurs by dissimilatory reduction and detoxification activities of microbes (Fitz and Wenzel, 2002) using As(V) as a terminal electron acceptor, and also As(V) reductase and As(III) extrusion by an As(III)-efflux pump (Cervantes et al., 1994).

6. Conclusions

The soil type, structure, properties, mineral components and pH may greatly affect the As-Pi interactions, mobility and availability of As in soils and uptake by plants with increased As availability and toxicity on sandy soil, but lower on a silty and sandy clay loam soils. Although all hydroponic studies indicated that Pi additions decreased As uptake by plant resulting in mitigating As toxicity, Pi application to soil either increased or decreased As uptake and toxicity effects by tolerant and non-tolerant plants depending on substrate conditions. What is the main reason behind these processes is not yet explained in any study. Therefore, this review hypothesized these processes as follows. The concentration of both Pi and As(V) in soil solution is typically orders of magnitude lower than the concentrations employed in the majority of hydroponic studies. For example, Wenzel et al. (2002) reported As(V) concentrations in the soil solutions from a range of uncontaminated and moderately contaminated soils to be ≤ 53 nM and up to 2.3 μM in a highly contaminated soil. Similarly, Pi concentrations in soil solution are typically < 10 μM (Bieleski, 1973), which again is orders of magnitude lower than the range of Pi concentrations employed in hydroponic experiments (e.g., Tu and Ma, 2003b, 202-1000 μM; Clark et al., 2000, 10-250 μM; Meharg et al., 1994, 25-1000 μM). Unrealistically high concentrations of Pi may elicit (low affinity) uptake pathways and metabolic processes which are not reflected in soil culture. Therefore, further hydroponic studies are recommended using the As and Pi concentrations that are commonly available in soil porewater.

In soils, Pi additions generally result in increased Pi and As uptake, and also increased As resistance indicating that increased levels of Pi in plant biomass reduced the toxicity effects of As. The effects of As(V) on Pi uptake are relatively weak due to high affinity of the transporters for Pi than As(V) in both hydroponics and soils. At low As(V) concentration, a high-Pi treatment decreased uptake and toxicity of As(V) in non-tolerants but not in As-tolerant plants. The As-tolerant plants might have distinct Pi uptake system with high selectivity for Pi and against As(V) resulting in higher Pi/As ratio and As resistance. New data analysis indicates that Pi addition promoted plant growth and As resistance not by reducing As uptake by plants, but increasing Pi concentrations in shoot and protective activity by internal P-induced metabolic reactions. Sulphur in soil can enhance As uptake by plants due to its ability to reduce the toxicity effects. The mycorrhizal association contributes to the increased Pi nutrition, plant growth and in ameliorating As toxicity. Microorganisms in the rhizosphere can cause transformation of As sepcies by redox reactions and methylation. The rhizobacteria release different types of acids to cause the dissolution of phosphate rock and minerals resulting in higher Pi nutrition and As uptake by plants.

7. Recommendations for future work

The previous studies related to As-Pi interactions in different substrates and the role of soil types on Pi and As(V) mobility and uptake by plants produced the contradictory results. Although the results from all hydroponic studies demonstrated the similar results, the studies conducted on soils showed a lot of discrepancies. Therefore, further research works are highly recommended to study the As-Pi interactions and uptake by plants grown in different soil types. After Pi addition to soil, higher Pi uptake and translocation from root to shoot can contribute to more resistance to As toxicity to plants than decreased As uptake. However, more detailed study is required to have a clear idea about how uptake of Pi ameliorates the As toxicity to plants. Several mechanisms for amelioration of As toxicity by AMF have been proposed and discussed in this review, and further research is needed to characterize these mechanisms, particularly a lack of As transport and increased Pi uptake via the AM pathway in plants. Since high Pi supply decreases mycorrhizal colonisation, proper management of Pi fertilization can increase the efficiency of mycorrhizae for enhanced Pi and a decreased As uptake. Therefore, this hypothesis should be further investigated in areas where --high As concentrations may exist in agricultural soils, irrigation water and/or groundwater. Using the isotopes can help to reveal these mechanisms as well.

Acknowledgements

This study received the financial support from the Australian Research Council Linkage project (LP110200961).

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Figure captions

Fig. 1. As-Pi interactions and uptake by plants in hydroponics. As and Pi supply variably control As and Pi uptake by plant roots. Pi supply strongly decreases As uptake, while As supply weakly decreases Pi uptake. Pi has higher affinity for plan roots than As.

Fig. 2. Mean shoot biomass, As and P concentrations in shoots and total As uptake by wheat plants grown in soil irrigated with As containing water at three concentrations amended and non-amended with P (data analysis from Pigna et al., 2009).

Fig. 3. Role of AM in modifying As-Pi interactions, and As and Pi uptake by plant root. The arbuscular mycorrhizal (AM) symbioses increase Pi uptake by plant roots and Pi/As ratio in shoot, while they decrease As uptake by roots.

Table 1

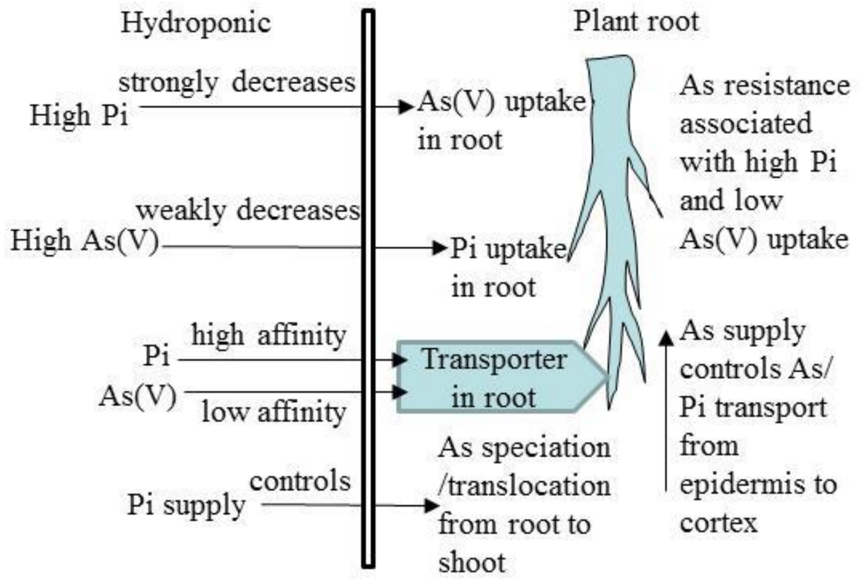
Effects of competition between As and Pi on uptake by plants grown in soil.

Soil types	Plant species	Addition	Effect	Reference
Soil	*Zea mays*	Fe (1-4 g/kg)	At low goethite - low As/high P uptake. At high goethite - no As/Pi uptake	Vetterlein et al. (2007)
Silt loam/ sand	*Zea mays*	Pi (50-300 mg/kg)	Pi had little effect on As toxicity to plants in silt loam, but enhanced As uptake and toxicity in sand at 80 mgAs/kg	Jacobs and Keeney (1970)
Soil	*Pteris vittata*	As (2.7-5.3mM)	Low As increased Pi uptake, but high As decreased Pi uptake. Pi increased plant biomass and As uptake at high As supply	Tu and Ma (2003a), Kertulis et al. (2005)
Soil	*Oryza sativa*	Pi	Increasing shoot Pi for breeding rice with low grain As	Lu et al. (2010)
Soil	*Oryza sativa*	Pi (0-0.5 mM)	Suppressed As(V), but not As(III) uptake; little difference in As uptake between two P-deprived rice genotypes	Abedin et al. (2002), Geng et al. (2006)
Clay loam	*T. durum*	Pi (75 kg/ha)	Prevented As uptake and translocation in plants	Pigna et al. (2010)
Soil	*H. vulgare*	Pi/ As	Pi strongly inhibited As(V) uptake. As weakly inhibited Pi uptake	Asher and Reay(1979)
Soil-sand, soil	*H. vulgare* *T. vulgare*	Pi (20-120 mg/kg)	Increased As uptake; decreased As(V) toxicity not by lowering As uptake, but by emhancing Pi nutrition. No competition between As and Pi.	Christophersen et al. (2009a), Tao et al. (2006)
Soil	*C. arietinum*	Pi (50-400)	Pi increased As uptake, but partially protected membranes from damage	Gunes et al. (2009)
Soil	*L. cinereus*	As/Pi	High level of As and low Pi supply decreased plant growth	Knudson et al. (2003)
Loam soil	*P. armeniaca*	Pi	Increased shoot and root As in soil contaminated with Pb-arsenate pesticide residue.	Creger & Peryea (1994)
Soil	*Arabidopsis thaliana*	Pi (10-40 mg/kg)	Low Pi supply increased As uptake and plant growth. High Pi supplydecreased As uptake due to competition on surface of soil particles and plant roots.	Geng et al. (2005)
Soil	*Solanum lycopersicum*	Pi (6 mM), As (4 mg/L)	Pi was more strongly adsorbed to soil than As(V), Pi desorbed As and increased As uptake by plants depending on soil charge properties	Pigna et al. (2012), Bolan et al. (2013)
Soil	*H. lanatus*	Pi (0.2 g/kg)	Increased As uptake by plant because of increased As desorption by competition	Lewińska and Karczewska (2013)
Soil	Plants	Pi	Enhanced As(V) and As(Ш) desorption from soil and thus leaching or uptake by plants	Fitz and Wenzel, 2002

As-Soil	Vegetable	Pi (3867)	Increased As uptake- 4.6–9.3 times forcarrot, 2.5–10for lettuce	Cao and Ma (2004)
Soil	No plants	Pi/As	At As:Pi ratio equal to 1, more Pi was sorbed than As. At As:Pi ratios > 1, Pi was desorbed due to a mass action effect	Woolson et al. (1973)
Fe-soil /mine soil	No plants	Pi	Reduced As(V) sorption to low Fe oxide soils and increased As mobility by competitive adsorption	Zupancic et al. (2012), Smith et al. (2002)

Table 2
Effect of competition between As and Pi on uptake by plants in hydroponics.

Plant species	Addition	Effect	References
Pteris vittata	Pi (0.1-2 mM)	High Pi decreased As(V) but not As(III) accumulation in roots/shoot; it enhanced As(V) reduction; high As(V) decreased Pi uptake	Lou et al. (2010), Tu et al. (2004), Wang et al. (2002)
Oryza sativa	Pi, 0.1 mM	High Pi concentration decreased As uptake; high As concentration slightly decreased Pi uptake	Lihong and Guilan (2009)
Holcus lanatus	Pi	Decreased As(V) uptake in nonresistant, but less in resistant plants	Meharg & MacNair (1992)
Lemna gibba	Pi, 40 mg/L	High Pi reduced As(V, III) uptake; high As reduced Pi uptake	Mkandawire et al. (2004)
M.sativa	Pi	Strongly suppressed As uptake	Khattak et al. (1991)
Silene vulgaris	Pi, 0.3-3 mg/L	As supply did not influence root growth at high Pi, but did at low Pi supply	Sneller et al. (1999)
Avena sativa	Pi	Decreased As(V) uptake, but little effect on As(III) uptake.	Rumberg et al. (1960)
Glycine max	As, 32-96 µM	Decreased Pi content in soybean organs	Milivojevic et al.(2006)
T. aestivum	Pi	High-affinity uptake system switched on at 25 mM Pi.	Zhu et al. (2006)



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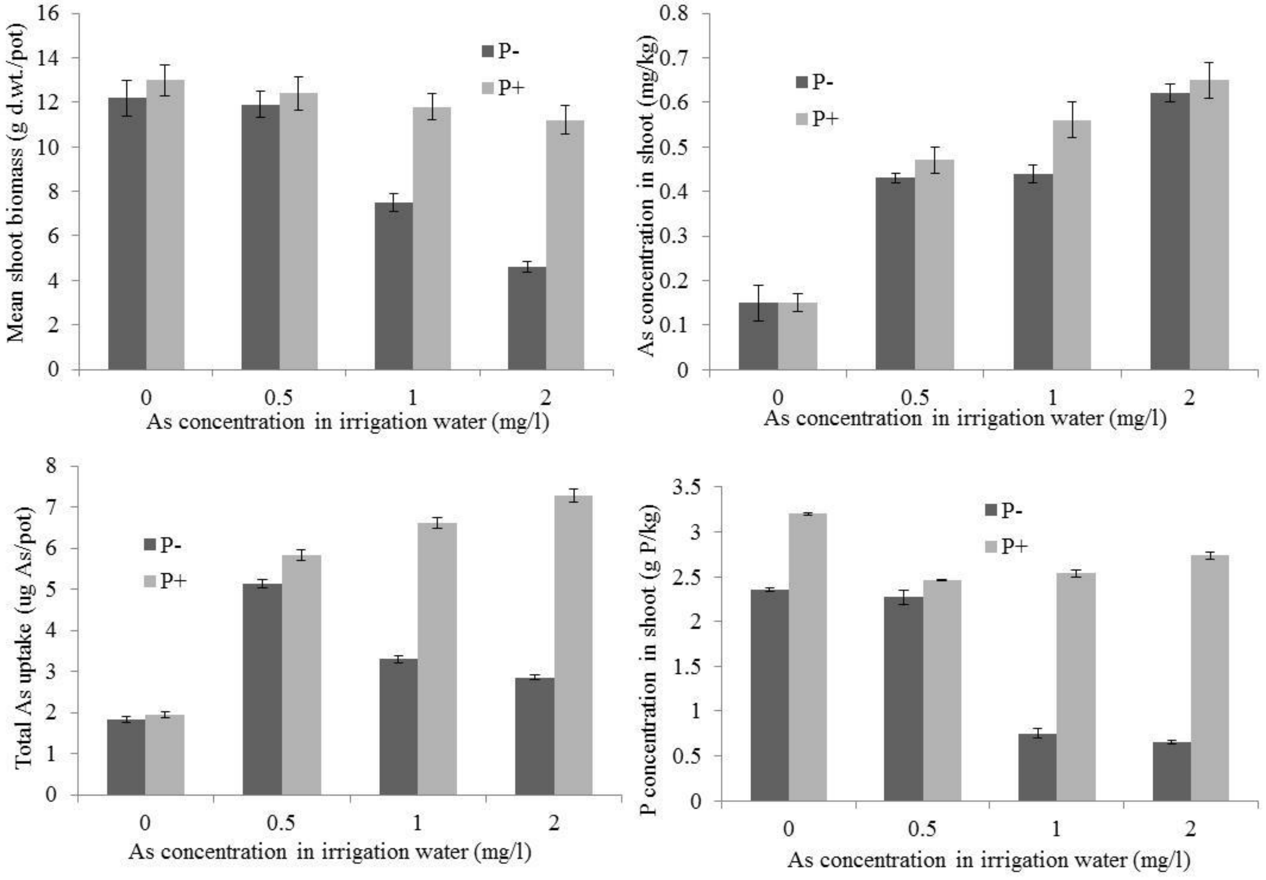

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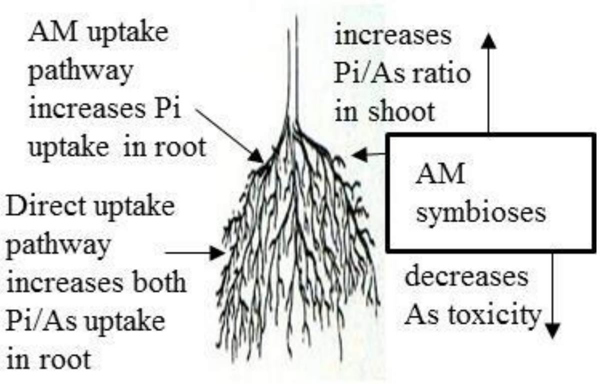

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