

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

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4 Hossain M Anawar^{a*}, Zed Rengel^a, Paul Damon^a, Mark Tibbett^b

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6 *^aSchool of Earth and Environment (M087), The University of Western Australia, Crawley WA
7 6009, Australia*

8 *^bCentre for Agri-Environmental Research & Soil Research Centre, School of Agriculture,
9 Policy and Development, University of Reading, RG6 6AR Reading, UK*

10

11 *Corresponding author

12 Phone +61-8-6488 1714

13 Fax +61-08-6488 1050

14 E-mail: anawar4@hotmail.com

15

16 ABSTRACT

17 High arsenic (As) concentrations in the soil, water and plant systems can pose a direct health
18 risk to humans and ecosystems. Phosphate (Pi) ions strongly influence As availability in soil,
19 its uptake and toxicity to plants. Better understanding of As(V)-Pi interactions in soils and
20 plants will facilitate a potential remediation strategy for As contaminated soils, reducing As
21 uptake by crop plants and toxicity to human populations via manipulation of soil Pi content.
22 However, the As(V)-Pi interactions in soil-plant systems are complex, leading to
23 contradictory findings among different studies. Therefore, this review investigates the role of
24 soil type, soil properties, minerals, Pi levels in soil and plant, Pi transporters, mycorrhizal

25 association and microbial activities on As-Pi interactions in soils and hydroponics, and uptake
26 by plants, elucidate the key mechanisms, identify key knowledge gaps and recommend new
27 research directions. Although Pi suppresses As uptake by plants in hydroponic systems, in
28 soils it could either increase or decrease As availability and toxicity to plants depending on
29 the soil types, properties and charge characteristics. In soil, As(V) availability is typically
30 increased by the addition of Pi. At the root surface, the Pi transport system has high affinity
31 for Pi over As(V). However, Pi concentration in plant influences the As transport from roots
32 to shoots. Mycorrhizal association may reduce As uptake via a physiological shift to the
33 mycorrhizal uptake pathway, which has a greater affinity for Pi over As(V) than the root
34 epidermal uptake pathway.

35

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

38

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

41

42 **Contents**

43 1. Introduction

44 *1.1. Arsenic in the environment*

45 *1.2. As-Pi chemistry and their competition*

46 *1.3. As-Pi interactions and significance of this review*

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

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

49 *3.1. Mechanisms of As toxicity to plants*

50 3.2. *As-Pi interactions and uptake by plants grown in soils*

51 3.3. *Impact of Pi availability on As uptake by plants in hydroponics*

52 3.4. *Relation of plant P status with As uptake*

53 3.5. *High-affinity and low-affinity Pi transporter for Pi and As uptake*

54 3.6. *Effect of root exudates on As and Pi uptake*

55 3.7. *Does As resistance occur via decreased As uptake or protective effect of high Pi uptake?*

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

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

58 6. Conclusions

59 7. Recommendations for future work

60 Acknowledgements

61 References

62

63 **1. Introduction**

64 *1.1. Arsenic in the environment*

65 Arsenic is generally considered one of the top priority elements for carcinogenicity and
66 toxicity to humans, animals and plants (ATSDR, 2007). Several severe incidents of As
67 poisoning have occurred in regions such as Bangladesh, India (West Bengal) (Anawar et al.,
68 2002), Vietnam, Taiwan and northwest China (Wang et al., 2002). Sources of high contents of
69 As in the environment are either geogenic in groundwater aquifers (Salmon et al., 2014) or
70 anthropogenic, typically associated with mining, industrial waste and agricultural chemicals
71 (Anawar et al., 2011). Average concentration of As in the Earth's crust is 1.5 µg/g with the
72 median value of 6.0 µg As /g for uncontaminated soils (Bowen, 1979). The average As
73 contents in agricultural fields that received As-containing pesticides and defoliants range from
74 5-2553 mg/kg (Walsh and Kenny, 1975). Early mining and smelting operations led to
75 contamination of the agricultural land, with soil As levels of 539-9380 mg/kg in Korea (Jung

76 et al., 2002), 11.1-651.1 mg/kg in Portugal (Pratas et al., 2005), etc. The As concentration in
77 human hair exhibits significant relationship with that in rice (*Oryza sativa* L.), wheat
78 (*Triticum aestivum* L.) and agricultural soils (Rahman et al., 2007, 2008) in As-affected areas
79 reflecting human exposure to As via the soil–plant transfer pathways (Geng et al., 2006;
80 Huang et al., 2006). These studies indicate widespread occurrence of As, and its
81 contamination effects on agricultural soils.

82

83 *1.2. As-Pi chemistry and their competition*

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

97

98 *1.3. As-Pi interactions and significance of this review*

99 A lot of research works have studied the As-Pi interactions in the environment with
100 conflicting results (Vetterlein et al., 2007; Zhao et al., 2009; Szegedi et al., 2010). On one

101 hand, Pi can decrease plant As uptake, and on the other hand, it may promote the availability
102 of As in soil and increase plant uptake. Therefore, it is necessary to explore the mechanism of
103 action between As and Pi under different environmental conditions. Most studies, to-date,
104 have failed to account for the complexity of interactions between Pi and As in soil-plant
105 system, and the variability in competition between As and Pi depending on soil types and
106 substrate conditions. Furthermore, the mechanisms of how Pi, when used as fertilizer,
107 ameliorate As toxicity to crop plants (Peryea, 1998) are not yet clear (Geng et al., 2005).
108 Although the major factors have been identified, the net effect of their interactions is poorly
109 understood. Therefore, further research is essential to assess the available knowledge, identify
110 the research gaps for the future work, understand the As-Pi interactions in soil-plant systems,
111 and their effects on exacerbation and/or amelioration of As toxicity, because these results can
112 help to decrease the risk of As toxicity to plants, animals and humans. Therefore, this study
113 reviewed (1) As-Pi interactions in soil-plant continuum, (2) the effect of soil type, soil
114 properties and minerals on As-Pi interaction in soils, (3) the role of different Pi transporters in
115 Pi and As uptake by plants, (4) the mechanisms of As and Pi uptake in As-tolerant and As-
116 intolerant plants, (5) how mycorrhizal symbioses and bacteria influence As and Pi uptake by
117 plants and As toxicity, and (6) case studies of As and Pi uptake by As-tolerant and As-
118 intolerant genotypes, and P-deficient and P-sufficient plants. This review investigates the role
119 of Pi on As uptake and toxicity to plants, elucidate the key mechanisms and factors affecting
120 the As : Pi interactions in soils and plants, identify key knowledge gaps and recommend new
121 research directions.

122

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

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

126 1973) making more As available by plant uptake (Zou et al., 2009). Due to slow sorption to
127 soil, Pi become more competitive than As(V) over time (Lambkin and Alloway, 2003).
128 According to the Steindorf-Rebhun-Sheintuch equation, ligand exchange theory and a share
129 charge hypothesis, Pi has more probability to replace As(V) from soils (Roy et al., 1986;
130 McBride, 1994). However, Pi could also be desorbed by As due to a mass action effect of
131 high As:Pi concentrations in soil solution (Lambkin and Alloway, 2003). The fast adsorption
132 of As and Pi occurred by exchange adsorption, while slow adsorption by specific adsorption
133 in the acid, neutral and calcareous purple soils (Zou et al., 2009).

134 The soil mineralogy, soil texture, soil properties and environmental factors that may
135 greatly affect the As-Pi interaction, mobility and availability of As in soils (Bissen and
136 Frimmel, 2003) and uptake by plants include mineral components, presence of anions (e.g.,
137 citrate, phosphate, phytates/phytic acid (Dalal, 1977; Marschner, 1995), residence time, pH,
138 redox potential, organic matter (OM), microbial activity and especially, Fe- and Al-oxide/
139 hydroxides (Melamed et al., 1995; Turpeinen et al., 1999; Fitz and Wenzel, 2002; Kubicki,
140 2005). Among these factors, goethite and pH strongly control the behaviour of As and Pi.
141 Knowledge of As(V) adsorption on individual soil minerals may predict As(V) adsorption in
142 whole soils and its response to Pi addition (Manning and Goldberg, 1996). Fordham and
143 Norrish (1979) and Violante and Pigna (2002) found that Fe and Mn-rich minerals such as
144 goethite, nontronite, ferruginous smectites, birnessite and pyrolusite absorbed more As(V)
145 than Pi when supplied in equal molar ratio, but more Pi than As(V) was sorbed on
146 noncrystalline Al containing minerals e.g., gibbsite, boehmite, allophane and clay fractions
147 (e.g., kaolinite, illite and vermiculite) resulting in higher As(V) desorption and uptake by
148 Indian mustard (*Brassica juncea* L.) (Bolan et al., 2013). A high rate of goethite addition to
149 soils can reduce Pi and As uptake by plants (Vetterlein et al., 2007). The Pi and Fe addition to

150 high As soils using a sequential incorporation method can significantly decrease As toxicity
151 to lettuce root growth by supplying a nutrient source (Koo et al., 2013).

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

164

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

166 *3.1. Mechanisms of As toxicity to plants*

167 The predominant effect of As toxicity in the cell is oxidative stress (Finnegan and Chen,
168 2012) that reduces seed germination, root and shoot growth and root surface area, etc. (Smith
169 et al., 2010), restrict nutrients and water uptake, and cause nutrient deficiency in plants
170 (Paivoke and Simola, 2001). After reduction arsenic (As(III)) forms chemical bond with
171 sulphhydryl groups and deactivates some enzymes (Delnomdedieu et al., 1993), and increases
172 reactive oxygen species and lipid peroxidation, but decreases the superoxide dismutase
173 activity and antioxidants levels (Raab et al., 2004) resulting in cellular membrane damage
174 (Mascher et al., 2002; Tuan et al., 2008). In contrast, Pi supply to As-treated plants decreased

175 activities of CAT, APX and lipid peroxidation, and thus decreased membrane damage (Gunes
176 et al., 2009). Arsenate in the cytoplasm competes with Pi forming unstable ADP-As(V), and
177 disrupt the energy flows in cells (Hartley-Whitaker et al., 2001, 2002). High S concentrations
178 in soil (e.g., via micronutrient fertilizers) alleviated the toxicity effect of As on plant growth
179 although Pi addition to soil enhanced As uptake by plants (Grifoni et al., 2015). This
180 phenomenon occurred due to formation of glutathione and phytochelatin, their chelation with
181 As and subsequent sequestration of these chelated complexes in the vacuoles (Cobbett, 2000;
182 Hartley-Whitaker et al., 2001). Although Pi supply suppressed the As uptake by plants in the
183 hydroponics, high S addition increased As uptake and decreased Pi content influencing the
184 As-Pi interaction in plants. Application of As and Zn to soils shows an antagonistic
185 relationship such as Zn in soils (at application rate of 3 mg/L) reduced As availability in soils
186 and uptake in plants (Sanchary and Huq, 2017). Arsenic accumulation by plants is controlled
187 by the oxidation state, As and P forms and plant species.

188 Arsenic hyperaccumulator plant species (e.g., *Pteris vittata*) detoxify As toxicity in a
189 number of ways such as transformation of As(V) to As(III) by enzyme and
190 compartmentalization in subcell; capturing reactive oxygen species by phytochelatin and
191 thiols, preventing lipid peroxidation (Shoji et al., 2008; Bona et al., 2011) and maintaining a
192 greater ratio of P/As in the roots, at least 1.2 in soil solution or 1.0 in fronds (Tu and Ma,
193 2003a; Singh and Ma, 2006). Therefore, Pi application may be an important strategy for As
194 detoxification, enhanced growth of *Pteris vittata* and efficient As uptake to phytoremediate
195 As-contaminated soils (Kertulis et al., 2005; Ye et al., 2011; Yan et al., 2012). The in-situ
196 measurement of As/Pi molar concentration ratio can predict As phytotoxicity, where As/Pi
197 ratio of 0.168–0.360 resulted in a 50% reduction of wheat (*Triticum aestivum*) growth
198 (Mojsilovic et al., 2011).

199

200 3.2. As-Pi interactions and uptake by plants grown in soils

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

218 The soil Pi status was related to As uptake by *Urtica dioica*, but not by *Phragmites*
219 *australis* indicating a differential response of plants to Pi (Ahmed et al., 2011). The uptake
220 kinetics of As and Pi by different plant species over short or long time vary depending on the
221 genus and species of plants. Therefore, further research is necessary to understand a time-
222 course of Pi and As(V) uptake by different plant species. Compared to non-tolerant *Holcus*
223 *lanatus*, the tolerant clones generally contained a higher proportion of As(V) (Quaghebeur
224 and Rengel, 2003). Arsenic uptake by and growth of rice cutgrass (*Leersia oryzoides* Sw.) and

225 tall fescue (*Festuca arundinacea* Schreb.) was not enhanced by P fertilization above a
226 minimal amount (Klaber and Barker, 2014). The application of Fe²⁺ to the rice fields under
227 flooded and reduced condition decreased the As uptake in rice grain and increased their yield,
228 while Pi application demonstrated the opposite results (Hossain et al., 2009).

229

230 3.3. Impact of Pi availability on As uptake by plants in hydroponics

231 Phosphate and As(V) interactions in hydroponics and plant accumulation are largely
232 investigated (Khattak et al., 1991; Clark et al., 2000; Pickering et al., 2000; Esteban et al.,
233 2003; Panuccio et al., 2012; Shaibur et al., 2013) and briefly summarized in Table 2 and Fig.
234 1. Most studies found that Pi deficiency in nutrient solutions increased the capacity of rice and
235 *Lemna gibba* plants to take up more Pi and As(V), but at low As concentration, high Pi
236 treatment decreased As(V) uptake and toxicity (Macnair and Cumbes, 1987; Mkandawire et
237 al., 2004; Lihong and Guilan, 2009; Panuccio et al., 2012) via suppression of the high-affinity
238 Pi/As(V) transport system. The supply of Pi also influenced the As speciation and transport
239 (Lei et al., 2012). The *Isatis cappadocica*, a robust perennial rosette plant, can grow in highly
240 impacted As-contaminated areas and hyperaccumulates As in its areal parts in hydroponic
241 media (Karimi and Souri, 2015).

242 Phosphate can suppress As(V) uptake in phytoplankton (Planas and Healey, 1978), *Oryza*
243 *sativa* (Abedin et al., 2002), *Lupinus albus* (Esteban et al., 2003), barley (Shaibur et al., 2013)
244 and As-tolerant species such as *Holcus lanatus*, *Cytisus striatus* (Meharg and MacNair, 1992;
245 Bleeker et al., 2003) and *Pteris vittata* (Wang et al., 2002; Tu and Ma, 2003b) grown in
246 hydroponic systems. The time-dependent split-Pi application (P₁₃₄₊₆₆ and P₆₆₊₁₃₄) with low
247 initial Pi application increased the growth of *Pteris vittata* L. and the efficiency of As
248 removal, that was higher than high initial Pi-supply (P₂₀₀₊₀) (Santos et al., 2008). The radial
249 loss of O₂ from aerenchyma structures converts the rice root surface into much more highly

250 oxidized condition compared to the surrounding environment (Colmer, 2003) and forms Fe-
251 oxide plaques on the root surface (Taylor et al., 1984).

252 The As-Pi interactions and their uptake by plants produced different and often
253 contradictory results depending on soil substrates and hydroponic conditions. The kinetics of
254 Pi and As accumulation in plants in hydroponics is overestimated compared to soil
255 experiments, because some processes such as water flow, redox potential, diffusion,
256 adsorption/desorption and ion exchange by minerals (Fe, Mn and Al oxyhydroxides, clay
257 minerals, sulfide minerals, etc.) and organic components are common in soil systems that
258 control As and Pi solubility and mobility in soils (Bissen and Frimmel, 2003; Anawar et al.,
259 2008), while these processes do not occur in hydroponics (Fitz and Wenzel, 2002). Hence, the
260 results from the hydroponic experiments can not be extrapolated to and may have limited
261 validity for soil-grown plants (Fitz and Wenzel, 2002). However, the hydroponics studies can
262 provide new knowledge on the membrane transport.

263

264 3.4. Relation of plant P status with As uptake

265 Quaghebeur and Rengel (2004) showed that P level in plant and As-Pi interactions in soil
266 are pivotal factors controlling As and P uptake by plants. The Pi deficiency can enhance As
267 uptake by plants e.g., *Pteris vittata* (Lei et al., 2012), P-deficient canola (Quaghebeur and
268 Rengel, 2004) and white lupin (*Lupinus albus*) (Esteban et al., 2003), causing a decline in
269 plant growth (Wang et al., 2002; Geng et al., 2006) except *Pteris vittata*. The low As uptake
270 and amelioration of As(V) toxicity in most of the +P plants occurs by competition with Pi
271 except lupin (Esteban et al., 2003; Reina et al., 2005). The P-deficient white lupin plants
272 develop proteoid roots and take up more Pi and As(V) (Esteban et al., 2003; Reina et al.,
273 2005), but lower translocation of As to shoot compared to corn plants (Vetterlein et al., 2009).
274 The presence of As(V) stimulated P uptake by P-deficient plants and reduced it for the P

275 sufficient ones. However, the concentration of As in rice and barley shoots grown in
276 hydroponics was very lower in P-deficient plants than in P-sufficient ones due to reddish iron
277 plaque formed on the root surface sequestering As and decreasing its uptake by roots (Chen et
278 al., 1980; Liu et al., 2004; Shaibur et al., 2013). Furthermore, it is assumed that high P level in
279 As-tolerant plants could alleviate As toxicity more efficiently than non-tolerant ones, and
280 despite the decreased As(V) uptake, As-tolerant plants might have higher total concentration
281 of As in their biomass over long time (Campos et al., 2014).

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

286

287 3.5. High-affinity and low-affinity Pi transporter for Pi and As uptake

288 The different families of transporter proteins are involved in Pi transport through plant
289 plasma membranes by a highly complex network of regulation, e.g., PHT1 transporters for Pi
290 accumulation from soil (Nussaume et al., 2011). Plants have developed different controlled
291 adaptative mechanisms to acquire necessary amount of external Pi and maintain Pi
292 homeostasis as well as overcome low Pi availability (reviewed in Schachtman et al., 1998;
293 Rouached et al., 2010). In the low Pi environment, Pi and As(V) accumulation by plants are
294 controlled by the Pht1;9 and Pht1;8 membrane transporters through activation of high-affinity
295 Pi transport system (Rausch and Bucher, 2002; Remy et al., 2012). Arsenate inhibited the root
296 growth of non-tolerant *Holcus lanatus* plants more strongly than the tolerant genotypes. The
297 tolerant plants (e.g., *Holcus lanatus*, *Silene vulgaris* and *Agrostis* species) took up less As(V)
298 than non-tolerant ones over short time (Porter and Peterson, 1977; Zhao et al., 2009)
299 supporting the hypothesis that a suppressed high-affinity Pi transport system provides As

300 resistance together with increased Pi/As ratio and strong selectivity against As(V) (Macnair
301 and Cumbes, 1987). However, total As accumulation is higher in tolerant than non-tolerant
302 plants over long time, as the latter become unhealthy and die relatively quickly (Puckett et al.,
303 2012).

304 As(V) and Pi compete for transporters across root plasma membrane (Smith et al., 2010).
305 Recently, Panuccio et al. (2012) indicated that As(V) resistance of *Pennisetum clandestinum*
306 Hochst (kikuyu perennial grass) occurs due to enhanced Pi nutrition, and not due to
307 downregulation of the Pi uptake system. Aquaglyceroporins (AQP3, AQP7, AQP9, and
308 AQP10) mediate the bidirectional movement of arsenite across cell membranes (Jung et al.,
309 2012). The As(III) transport was not affected by Pi in rice.

310

311 *3.6. Effect of root exudates on As and Pi uptake*

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

320

321 *3.7. Does As resistance occur via decreased As uptake or protective effect of high Pi uptake?*

322 Arsenic tolerance in higher plants hinges on decreased As accumulation by suppression of
323 the high-affinity Pi/As(V) uptake system in roots (Meharg and Macnair, 1992) and decreased
324 As transport to shoots (Pigna et al., 2009), both of which are dependent on high shoot Pi

325 status that outcompetes As in metabolic reactions as reported for the *ars1* Arabidopsis
326 mutants (Lee et al., 2003) and vacuolar sequestration of As in shoots. However, our data
327 analysis from Pigna et al. (2009, 2010) and Lewinska and Karczewska (2013) demonstrate the
328 new results as follows: Pi application to soils not only augmented plant growth, but also
329 increased As and Pi concentrations in shoot of wheat (*Triticum durum* L.) irrigated with As-
330 rich water (Fig. 2). Therefore, it is clear that Pi addition to soils alleviated As toxicity not by
331 decreasing As uptake by plants, but increasing the plant biomass, Pi nutrition and metabolic
332 reactions. Joardar and Kawai (2014) and Christophersen et al. (2009a) also reported that the
333 decreased As toxicity occurred not due to lower As uptake by plants, but increased Pi uptake
334 by plant root surface and transport to shoot (Campos et al., 2014). A more detailed
335 investigation of uptake of As(V) and Pi is necessary to clarify this hypothesis. Our recent
336 study indicated that P addition to topsoil (upper 5 cm) of three-layered soil system with As in
337 the subsoil (> 10 cm) was a more effective strategy to improve the plant growth by alleviating
338 As toxicity, increasing P concentration, but reducing As level in plant biomass than P
339 application in subsoil (Anawar et al., 2016).

340

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

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

350 Based on demonstrated studies it is reported that AM plant roots may have physiologically
351 altered Pi uptake systems, whereby there is a switch from the epidermal uptake pathway to an
352 AM uptake pathway following colonisation. Considering the physiological and molecular
353 evidence, Smith et al. (2003) showed that AM plants have two pathways for Pi and As(V)
354 uptake: direct pathway via high-affinity Pi transporters Pht1;1 and Pht1;2 in the epidermis and
355 root hairs in AM and NM (non-mycorrhizal) plants (Schunmann et al., 2004a,b; Shin et al.,
356 2004) regardless of their responsiveness (Smith et al., 2010). The down-regulation of
357 expression of high-affinity Pi-uptake pathway lowered Pi and As(V) uptake in AM barley and
358 genotypes of As-tolerant *Holcus lanatus*, but other studies indicated no such effect (Grace et
359 al., 2009). However, it suggested that the AM and direct Pi uptake pathways are integrated,
360 and Pi and As(V) uptake may be inter-dependent (Smith et al., 2003, 2004; Smith and Read,
361 2008), although details of the mechanisms are still unclear.

362 The transporters in external hyphae of the AM fungi in symbiosis condition uptake Pi via
363 the mycorrhizal pathway (Maldonado-Mendoza et al., 2002). The hyphae transports Pi along
364 a long way (Ezawa et al., 2002) and transfer to plant across a symbiotic interface to cortical
365 cells by induction of Pht1;8 in roots (Paszkowski et al., 2002; Glassop et al., 2005). Thus, a
366 higher amount of Pi and exclusion of As are promoted by the AM pathway that protect plants
367 against As uptake and toxicity (Christophersen et al., 2009b). It suggested that AMF
368 decreased As toxicity in soil by converting As speciation from inorganic to organic forms by
369 hyphae-produced glomalin (Ultra Jr et al., 2007; Chern et al., 2007; Smith and Read, 2008)
370 and acting as a barrier for As uptake (Ultra Jr et al., 2007; Ahmed et al., 2011) through several
371 physical mechanisms: adsorption onto plant or fungal cell walls in plant tissues or extra-
372 radical mycelium in soil (Hildebrandt et al., 1999; Kaldorf et al., 1999; Joner et al., 2000);
373 exclusion by precipitation onto polyphosphate granules (Turnau et al., 1993). Some studies
374 reported that lower As uptake in shoot occurred mainly due to a “dilution effect” from

375 increased growth of AM plants and decreased As partitioning to shoots, rather than decreased
376 As uptake per plant (Chen et al., 2007; Zhao et al., 2009; Ahmed et al., 2011). Therefore,
377 further research is needed to determine the effects of AM fungi-induced various metabolic
378 strategies for As resistance mechanism and As uptake by plants. A recent study suggests that
379 mycorrhizal colonization converts As into non-toxic complexes by enhancing the production
380 of cysteine, glutathione, non-protein thiols, and activity of glutathione-S-transferase in plants
381 indicating the multifarious role of AMF in alleviation of As toxicity (Sharma et al., 2017).
382 Furthermore, Pi from superphosphate fertilizer or other sources may suppress the AMF
383 colonization, change the structure of the AMF community (Shetty et al., 1995; Ahmed et al.,
384 2011) and thus strongly influence any potential AM effect on As resistance. Combined
385 application of inoculum and Pi to soil augmented plant biomass, reduced As toxicity and
386 increased plant Pi nutrition; and these effects were higher than inoculation only with native
387 AMF (Cozzolino et al., 2010; Cattani et al., 2015).

388 *Glomus mosseae* that was more tolerant and unaffected by the high concentrations of As
389 (e.g., 200 mg/kg) than *Medicago truncatula* plant, increased host plant As tolerance and Pi
390 nutrition (Xu et al., 2008). Not only AMF, but also ericoid and ectomycorrhizal fungi can
391 increase their tolerance to As(V) contamination via different mechanisms (Sharples et al.,
392 1999, 2000a). The ericoid mycorrhizal fungus *Hymenoscyphus ericae* from an As and Cu
393 mine spoil has adapted to As(V) contamination by decreasing As uptake via enhanced As(III)
394 efflux (Sharples et al., 2000b), but the mechanisms behind this process are still unclear. Three
395 species of ectomycorrhizal fungi showed variable response to arsenate toxicity under the
396 influence of PO_4^{3-} concentration (Chen and Tibbett, 2007). The *Suillus variegatus* and
397 *Hebeloma crustuliniforme* exhibited the high sensitivity to As toxicity at low Pi treatments,
398 while the higher Pi treatments reduced As toxicity. In contrast, the *Cenococcum*

399 *geophilum* exhibited higher tolerance to As; and Pi did not show ameliorating effect on
400 As toxicity in *C. geophilum*.

401

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

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

417

418 **6. Conclusions**

419 The soil type, structure, properties, mineral components and pH may greatly affect the As-
420 Pi interactions, mobility and availability of As in soils and uptake by plants with increased As
421 availability and toxicity on sandy soil, but lower on a silty and sandy clay loam soils.
422 Although all hydroponic studies indicated that Pi additions decreased As uptake by plant
423 resulting in mitigating As toxicity, Pi application to soil either increased or decreased As

424 uptake and toxicity effects by tolerant and non-tolerant plants depending on substrate
425 conditions. What is the main reason behind these processes is not yet explained in any study.
426 Therefore, this review hypothesized these processes as follows. The concentration of both Pi
427 and As(V) in soil solution is typically orders of magnitude lower than the concentrations
428 employed in the majority of hydroponic studies. For example, Wenzel et al. (2002) reported
429 As(V) concentrations in the soil solutions from a range of uncontaminated and moderately
430 contaminated soils to be ≤ 53 nM and up to 2.3 μ M in a highly contaminated soil. Similarly,
431 Pi concentrations in soil solution are typically < 10 μ M (Bielecki, 1973), which again is orders
432 of magnitude lower than the range of Pi concentrations employed in hydroponic experiments
433 (e.g., Tu and Ma, 2003b, 202-1000 μ M; Clark et al., 2000, 10-250 μ M; Meharg et al., 1994,
434 25-1000 μ M). Unrealistically high concentrations of Pi may elicit (low affinity) uptake
435 pathways and metabolic processes which are not reflected in soil culture. Therefore, further
436 hydroponic studies are recommended using the As and Pi concentrations that are commonly
437 available in soil porewater.

438 In soils, Pi additions generally result in increased Pi and As uptake, and also increased As
439 resistance indicating that increased levels of Pi in plant biomass reduced the toxicity effects of
440 As. The effects of As(V) on Pi uptake are relatively weak due to high affinity of the
441 transporters for Pi than As(V) in both hydroponics and soils. At low As(V) concentration, a
442 high-Pi treatment decreased uptake and toxicity of As(V) in non-tolerants but not in As-
443 tolerant plants. The As-tolerant plants might have distinct Pi uptake system with high
444 selectivity for Pi and against As(V) resulting in higher Pi/As ratio and As resistance. New
445 data analysis indicates that Pi addition promoted plant growth and As resistance not by
446 reducing As uptake by plants, but increasing Pi concentrations in shoot and protective activity
447 by internal P-induced metabolic reactions. Sulphur in soil can enhance As uptake by plants
448 due to its ability to reduce the toxicity effects. The mycorrhizal association contributes to the

449 increased Pi nutrition, plant growth and in ameliorating As toxicity. Microorganisms in the
450 rhizosphere can cause transformation of As species by redox reactions and methylation. The
451 rhizobacteria release different types of acids to cause the dissolution of phosphate rock and
452 minerals resulting in higher Pi nutrition and As uptake by plants.

453

454 **7. Recommendations for future work**

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

471

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475
476 **References**

- 477 Abedin, M.J., Feldmann, J., Meharg, A.A., 2002. Uptake kinetics of arsenic species in rice
478 plants. *Plant Physiology* 128, 1120–1128.
- 479 Ahmed, F.R.S., Killham, K., Alexander, I., 2006. Influences of arbuscular mycorrhizal fungus
480 *Glomus mosseae* on growth and nutrition of lentil irrigated with arsenic contaminated
481 water. *Plant and Soil* 283, 33–41.
- 482 Ahmed, F.R.S., Alexander, I.J., Mwinyihija, M., Killham, K., 2011. Effect of superphosphate
483 and arbuscular mycorrhizal fungus *Glomus mosseae* on phosphorus and arsenic uptake in
484 lentil (*Lens culinaris* L.). *Water Air Soil Pollution* 221, 169–182.
- 485 Anawar, H.M., Akai, J., Mostofa, K.M.G., Safiullah, S., Tareq, S.M., 2002. Arsenic poisoning
486 in groundwater: health risk and geochemical sources in Bangladesh. *Environment*
487 *International* 27, 597-604.
- 488 Anawar, H.M., Garcia-Sanchez, A., Santa-Regina, I., 2008. Evaluation of various chemical
489 extraction methods to estimate plant-available arsenic in mine soils. *Chemosphere* 70,
490 1459-1467.
- 491 Anawar, H.M., Akai, J., Mihaljevič, M., Sikder, A.M., Ahmed, G., Tareq, S.M., Rahman,
492 M.M., 2011. Arsenic contamination in groundwater of Bangladesh: perspectives on
493 geochemical, microbial and anthropogenic issues. *Water* 3, 1050-1076.
- 494 Anawar, H.M., Damon, P., Rengel, Z., Jasper, D.A., Tibbett, M., 2016. Alleviating arsenic
495 toxicity to plants in a simulated cover system with phosphate placement in topsoil and
496 subsoil. In: AB Fourie & M Tibbett (eds), *Proceedings of the 11th International*
497 *Conference on Mine Closure*, Australian Centre for Geomechanics, Perth, pp. 555-565.
- 498 Asher, C.J., Reay, P.F., 1979. Arsenic uptake by barley seedlings. *Australian Journal of Plant*
499 *Physiology* 6, 459-466.
- 500 ATSDR (Agency for Toxic Substances and Disease Registry), 2007. Toxicological profile for
501 arsenic. Atlanta, GA: U.S. Department of Health and Human Services, Public Health
502 Service.
- 503 Bielecki, R.L., 1973. Phosphate pools, phosphate transport, and phosphate availability.
504 *Annual Review in Plant Physiology* 24, 225-252.

505 Bissen, M., Frimmel, F.H., 2003. Arsenic — a review. Part I: Occurrence, toxicity, speciation,
506 mobility. Acta hydrochim. Hydrobiologia 31(1), 9–18.

507 Bleeker, P.M., Schat, H., Vooijs, R., Verkleij, J.A.C., Ernst, W.H.O., 2003. Mechanisms of
508 arsenate resistance in *Cytisus striatus*. New Phytology 157, 33-38.

509 Bolan, N., Mahimairaja, S., Kunhikrishnan, A., Choppala, G., 2013. Phosphorus–arsenic
510 interactions in variable-charge soils in relation to arsenic mobility and bioavailability.
511 Science of the Total Environment 463-464, 1154-1162.

512 Bona, E., Marsano, F., Massa, N., Cattaneo, C., Cesaro, P., Argese, E., Toppi, L.S., Cavalett,
513 M., Berta, G., 2011. Proteomic analysis as a tool for investigating arsenic stress in *Pteris*
514 *vittata* roots colonized or not by arbuscular mycorrhizal symbiosis. Journal of Proteomics
515 74, 1338 -1350.

516 Bowen, H.J.M., 1979. Environmental Chemistry of the Elements. Academic Press, London.

517 Cai, L., Liu, G., Rensing, C., Wang, G., 2009. Genes involved in arsenic transformation and
518 resistance associated with different levels of arsenic-contaminated soils. BMC
519 Microbiology 9, 4.

520 Campos, N.V., Loureiro, M.E., Azevedo, A.A., 2014. Differences in phosphorus
521 translocation contributes to differential arsenic tolerance between plants of *Borreria*
522 *verticillata* (Rubiaceae) from mine and non-mine sites. Environmental Science and
523 Pollution Research 21, 5586-5596.

524 Cao, X., Ma, L.Q., 2004. Effects of compost and phosphate on plant arsenic accumulation
525 from soils near pressure treated wood. Environmental Pollution 132, 435–442.

526 Cattani, I., Beone, G.M., Gonnelli, C., 2015. Influence of *Rhizophagus irregularis* inoculation
527 and phosphorus application on growth and arsenic accumulation in maize (*Zea mays* L.)
528 cultivated on an arsenic-contaminated soil. Environmental Science and Pollution Research
529 22, 6570-6577.

530 Chen, B., Xiao, X., Zhu, Y.-G., Smith, F.A., Xie, Z.M., Smith, S.E., 2007. The arbuscular
531 mycorrhizal fungus *Glomus mosseae* gives contradictory effects on phosphorus and arsenic
532 acquisition by *Medicago sativa* Linn. Science of the Total Environment 379, 226–234.

533 Chen, S.H., Tibbett, M., 2007. Phosphate supply and arsenate toxicity in ectomycorrhizal
534 fungi. Journal of Basic Microbiology 47, 358-362.

535 Chen, C.C., Dixon, J.B., Turner, F.T., 1980. Iron coating on rice root: morphology and model
536 of development. Soil Science Society of America Journal 44, 1113–1119.

537 Chern, E.C., Tsai, D.W., Ogunseitan, O.A., 2007. Deposition of glomalin-related soil protein
538 and sequestered toxic metals into watersheds. *Environmental Science and Technology* 41,
539 3566–3572.

540 Christophersen, H.M., Smith, S.E., Pope, S., Smith, F.A., 2009a. No evidence for competition
541 between As(V) and phosphate for uptake from soil by medic or barley. *Environment*
542 *International* 35, 485–490.

543 Christophersen, H.M., Smith, F.A., Smith S.E., 2009b. Arbuscular mycorrhizal colonization
544 reduces As(V) uptake in barley via downregulation of transporters in the direct epidermal
545 phosphate uptake pathway. *New Phytologist* 184, 962-974.

546 Clark, G.T., Dunlop, J., Phung, H.T., 2000. Phosphate absorption by *Arabidopsis thaliana*:
547 interactions between phosphorus status and inhibition by arsenate. *Australian Journal of*
548 *Plant Physiology* 27, 959–965.

549 Cobbett, C.S., 2000. Phytochelatins and their roles in heavy metal detoxification. *Plant*
550 *Physiology* 123, 825–832.

551 Colmer, T.D., 2003. Long-distance transport of gases in plants: a perspective on internal
552 aeration and radial oxygen loss from roots. *Plant Cell Environment* 26, 17–36.

553 Cozzolino, V., Pigna, M., Di Meo, V., Caporale, A.G., Violante, A., 2010. Effects of
554 arbuscular mycorrhizal inoculation and supply on the growth of *Lactuca sativa* L. and
555 arsenic and phosphorus availability in an arsenic polluted soil under non-sterile conditions.
556 *Applied and Soil Ecology* 45, 262-268.

557 Creger, T., Peryea, F., 1994. Phosphate fertilizer enhances arsenic uptake by apricot liners
558 grown in lead-As(V)-enriched soil. *Horticulture Science* 29, 88–92.

559 Dalal, R.C., 1977. Soil organic phosphorus. *Advances in Agronomy* 29, 85-117.

560 Delnomdedieu, M., Basti, M.M., Otvos, J.D., Thomas, D.J., 1993. Transfer of As(III) from
561 glutathione to dithiols: A model of interaction. *Chemical Research and Toxicology* 6, 598–
562 602.

563 Dunlop, J., Phung, H.T., Meeking, R., White, D.W.R., 1997. The kinetics associated with
564 phosphate absorption by *Arabidopsis* and its regulation by phosphorus status. *Australian*
565 *Journal of Plant Physiology* 24, 623–629.

566 Duponnois, R., Colombet, A., Hien, V., Thioulouse, J., 2005. The mycorrhizal fungus *Glomus*
567 *intraradices* and rock phosphate amendment influence plant growth and microbial activity
568 in the rhizosphere of *Acacia holosericea*. *Soil Biology and Biochemistry* 37, 1460–1468.

569 Esteban, E., Carpena, R.O., Meharg, A.A., 2003. High-affinity phosphate/As(V) transport in
570 white lupin (*Lupinus albus*) is relatively insensitive to phosphate status. *New Phytologist*
571 158, 165–173.

572 Ezawa, T., Smith, S.E., Smith, F.A., 2002. P metabolism and transport in AM fungi. *Plant and*
573 *Soil* 244, 221–230.

574 Fitz, W.J., Wenzel, W.W., 2002. Arsenic transformations in the soil-rhizosphere-plant
575 system: fundamentals and potential application to phytoremediation. *Journal of*
576 *Biotechnology* 99, 259-278.

577 Finnegan, P.M., Chen, W., 2012. Arsenic toxicity: the effects on plant metabolism. *Frontier in*
578 *Physiology* 3, 182.

579 Fordham, A.W., Norrish, K., 1979. Arsenate-73 uptake by components of several acidic soils
580 and its implications for phosphate retention. *Australian Journal of Soil Research* 17, 307–
581 316.

582 Geng, C.N., Zhu, Y.G., Tong, Y.P., Christie, P., 2005. Uptake and translocation of arsenic
583 and phosphorus in pho2 mutant and wild type of *Arabidopsis thaliana*. *Journal of Plant*
584 *Nutrition* 28, 1323-1336.

585 Geng, C.N., Zhu, Y.G., Hu, Y., Williams, P., Meharg, A.A., 2006. Arsenate causes
586 differential acute toxicity to two P-deprived genotypes of rice seedlings (*Oryza sativa* L.).
587 *Plant and Soil* 279, 297–306.

588 Ghosh, P., Rathinasabapathi, B., Ma, L.Q., 2015. Phosphorus solubilization and plant growth
589 enhancement by arsenic-resistant bacteria. *Chemosphere* 134, 1-6.

590 Glassop, D., Smith, S.E., Smith, F.W., 2005. Cereal phosphate transporters associated with
591 the mycorrhizal pathway of phosphate uptake into roots. *Planta* 222, 688–698.

592 Grace, E.J., Cotsaftis, O., Smith, F.A. et al., 2009. Arbuscular mycorrhizal inhibition of
593 growth in barley cannot be attributed to extent of colonisation, fungal P uptake or effects
594 on plant phosphate transporter expression. *New Phytologist* 181, 938–949.

595 Grifoni M, Schiavon M, Pezzarossa B, Petruzzelli G, Malagoli M (2015) Effects of
596 phosphate and thiosulphate on arsenic accumulation in the species *Brassica juncea*.
597 *Environmental Science and Pollution Research* 22, 2423-2433.

598 Gunes, A., Pilbeam, D. J., Inal, A., 2009. Effect of arsenic–phosphorus interaction on arsenic-
599 induced oxidative stress in chickpea plants. *Plant and Soil* 314, 211–220.

600 Hanada, S., Nakano, M., Saitoh, H., Mochizuki, T., 1975. Studies on the pollution of apple
601 orchard surface soils and its improvement in relation to inorganic spray residues. I.
602 *Bulletin of Faculty of Agriculture, Hirosaki University* 25, 13–17.

603 Hartley-Whitaker, J., Ainsworth, G.C., Meharg, A.A., 2001. Copper-and arsenate-induced
604 oxidative stress in *Holcus lanatus* L. clones with differential sensitivity. *Plant Cell and*
605 *Environment* 24, 713–722.

606 Hartley-Whitaker, J., Woods, C., Meharg, A.A., 2002. Is differential phytochelatin production
607 related to decreased arsenate influx in arsenate tolerant *Holcus lanatus*? *New Phytologist*
608 155, 219–225.

609 Hildebrandt, U., Kaldorf, M., Bothe, H., 1999. The zinc violet and its colonization by
610 arbuscular mycorrhiza fungi. *Journal of Plant Physiology* 154, 709–717.

611 Hossain, M.B., Jahiruddin, M., Loeppert, R.H., Panaullah, G.M., Islam, M.R., Duxbury, J.M.,
612 2009. The effects of iron plaque and phosphorus on yield and arsenic accumulation in
613 rice. *Plant and Soil* 317, 167-176.

614 Huang, R.-Q., Gao, S.-F., Wang, W.-L., Staunton, S., Wang, G., 2006. Soil arsenic
615 availability and the transfer of soil arsenic to crops in suburban areas in Fujian Province,
616 southeast China. *Science of the Total Environment* 368, 531–541.

617 Jacobs, L.W., Keeney, D.R., 1970. Arsenic - phosphorus interactions on corn.
618 *Communications in Soil Science and Plant Analysis* 1, 85-93.

619 Joardar J, Kawai S (2014) Phosphate rich soil additive baked pig manure effectively reduces
620 arsenic concentration in Japanese mustard spinach (*Brassica rapa* var. *perviridis*) grown
621 with arsenic contaminated irrigation water. *American Journal of Experimental Agriculture*
622 4, 142-152.

623 Joner, E.J., Briones, R., Leyval, C., 2000. Metal-binding capacity of arbuscular mycorrhizal
624 mycelium. *Plant and Soil* 226, 227–234.

625 Jung, D., MacIver, B., Jackson, B.P., Barnaby, R., Sato, J.D., Zeidel, M.L., Shaw, J.R.,
626 Stanton, B.A., 2012. A novel aquaporin 3 in killifish (*Fundulus heteroclitus*) is not an
627 arsenic channel. *Toxicological Science* 127, 101–109.

628 Jung, MC, Thornton I and Chon, H-T. 2002. Arsenic, Sb and Bi contamination of soils,
629 plants, waters and sediments in the vicinity of the Dalsung Cu–W mine in Korea. *Sci Total*
630 *Environ*, 295, 81-89.

631 Kaldorf, M., Kuhn, A. J., Schroder, W. H., Hildebrandt, U., Bothe, H., 1999. Selective
632 element deposits in maize colonized by a heavy metal resistance conferring arbuscular
633 mycorrhizal fungus. *Journal of Plant Physiology* 154, 718–728.

634 Karimi, N., Souri, Z., 2015. Effect of phosphorus on arsenic accumulation and
635 detoxification in arsenic hyperaccumulator, *Isatis cappadocica*. *Journal of Plant Growth*
636 *Regulation* 34, 88-95.

637 Kertulis, G.M., Ma, L.Q., MacDonald, G.E., Chen, R., Winefordner, J.D., Cai, Y., 2005.
638 Arsenic speciation and transport in *Pteris vittata* L. and the effects on phosphorus in the
639 xylem sap. *Environmental and Experimental Botany* 54, 239–247.

640 Khattak, R.A., Page, A.L., Parker, D.R., Bakhtar, D., 1991. Accumulation and interactions of
641 arsenic, selenium, molybdenum and phosphorus in alfalfa. *Journal of Environmental*
642 *Quality* 20, 165–168.

643 Klaber, N.S., Barker, A.V., 2014. Accumulation of phosphorus and arsenic in two perennial
644 grasses for soil remediation. *Communications in Soil Science and Plant Analysis* 45, 810-818.

645 Knudson, J.A., Meikle, T., DeLuca, T.H., 2003. Role of mycorrhizal fungi and phosphorus in
646 the arsenic resistance of basin wildrye. *Journal of Environmental Quality* 32, 2001–2006.

647 Koo, N., Kim, M.-S., Hyun, S., Kim, J.-G., 2013. Effects of the incorporation of phosphorus
648 and iron into arsenic-spiked artificial soils on root growth of lettuce using response surface
649 methodology. *Communications in Soil Science and Plant Analysis* 44, 1259-1271.

650 Lambkin, D.C., Alloway, B.J., 2003. As(V) -induced phosphate release from soils and its
651 effect on plant phosphorus. *Water, Air, and Soil Pollution* 144, 41–56.

652 Lee, D.A., Chen, A., Schroeder, J.I., 2003. *Ars1*, an *Arabidopsis* mutant exhibiting increased
653 resistance to arsenate and increased phosphate uptake. *Plant Journal* 35, 637-646.

654 Lei, M., Wan, X.-M., Huang, Z.-C., Chen, T.-B., Li, X.-W., Liu, Y.-R., 2012. First evidence
655 on different transportation modes of arsenic and phosphorus in arsenic hyperaccumulator
656 *Pteris vittata*. *Environmental Pollution* 161, 1-7.

657 Lessl, J.T., Ma, L.Q., 2013. Sparingly-soluble phosphate rock induced significant plant
658 growth and arsenic uptake by *Pteris vittata* from three contaminated soils. *Environmental*
659 *Science and Technology* 47(10), 5311–5318.

660 Lessl, J.T., Luo, J., Ma, L.Q., 2014. *Pteris vittata* continuously removed arsenic from non-
661 labile fraction in three contaminated-soils during 3.5 years of phytoextraction. *Journal of*
662 *Hazardous Materials* 279, 485-492.

663 Lewinska, K., Karczewska, A., 2013. Influence of soil properties and phosphate addition on
664 arsenic uptake from polluted soils by velvet grass (*Holcus lanatus*). *International Journal of*
665 *Phytoremediation* 15, 91-104.

666 Li, H.Y., Smith, S.E., Holloway, R.E. et al., 2006. Arbuscular mycorrhizal fungi contribute to
667 phosphorus uptake by wheat grown in a phosphorus-fixing soil even in the absence of
668 positive growth responses. *New Phytologist* 172, 536–543.

669 Li, R.-Y., Ago, Y., Liu, W.-J., Mitani, N., Feldmann, J., McGrath, S.P., Ma, J.F., Zhao, F.-J.,
670 2009. The rice aquaporin Lsi1 mediates uptake of methylated arsenic species. *Plant*
671 *Physiology* 150, 2071–2080.

672 Lihong, W., Guilan, D., 2009. Effect of external and internal phosphate status on arsenic
673 toxicity and accumulation in rice seedlings. *Journal of Environmental Science* 21, 346–
674 351.

675 Liu, W.-J., Zhu, Y.-G., Smith, F.A., Smith, S.E., 2004. Do phosphorus nutrition and iron
676 plaque alter As(V) uptake by rice seedlings in hydroponic culture? *New Phytologist* 162,
677 481–488.

678 Lombi, E., Wenzel, W.W., Sletten, R., 1999. Arsenic adsorption by soil and iron-coated sand:
679 kinetics and reversibility. *Journal of Plant Nutrition and Soil Science* 162, 451-456.

680 Lou, L., Ye, Z., Lin, A., Wong, M., 2010. Interaction of arsenic and phosphate on their uptake
681 and accumulation in Chinese brake fern. *International Journal of Phytoremediation* 12,
682 487–502.

683 Lu, Y., Dong, F., Deacon, C., Chen, H.-J., Raab, A., Meharg, A.A., 2010. Arsenic
684 accumulation and phosphorus status in two rice (*Oryza sativa* L.) cultivars surveyed from
685 fields in South China. *Environmental Pollution* 158, 1536–1541.

686 Ma, J.F., Yamaji, N., Mitani, N., Xu, X.-Y., Su, Y.-H., McGrath, S.P., Zhao, F.-J., 2008.
687 Transporters of arsenite in rice and their role in arsenic accumulation in rice grain.
688 *Proceedings of National Academy of Science, USA* 105, 9931–9935.

689 Maldonado-Mendoza, I.E., Dewbre, G.R., van Buuren, M.L., Versaw, W., Harrison, M.J.,
690 2002. Methods to estimate the proportion of plant and fungal RNA in an arbuscular
691 mycorrhizal fungus. *Mycorrhiza* 12, 67–74.

692 Marschner, H., 1995, *Mineral Nutrition of Higher Plants*, 2nd ed., Academic Press, London,
693 889 pp.

694 Mascher, R., Lippmann, B., Holzinger, S. et al., 2002. Arsenate toxicity: effects on oxidative
695 stress response molecules and enzymes in red clover plants. *Plant Science* 163, 961–969.

696 McBride, M.B., 1994. *Environmental Chemistry of Soils*, Oxford University Press, UK.

697 Meharg, A.A., MacNair, M.R., 1992. Suppression of the high affinity phosphate uptake
698 system: A mechanism of As(V) resistance in *Holcus lanatus* L. *Journal of Experimental*
699 *Botany* 43, 519–524.

700 Meharg, A.A., Naylor, J., Macnair, M.R., 1994. Phosphorus nutrition of arsenate-tolerant and
701 nontolerant phenotypes of velvet grass. *Journal of Environmental Quality* 23, 234–238.

702 Meharg, A.A., Hartley-Whitaker, J., 2002. Arsenic uptake and metabolism in arsenic resistant
703 and non resistant plant species. *New Phytologist* 154, 29–43.

704 Melamed, R., Jurinak, J.J., Dudley, L.M., 1995. Effect of adsorbed phosphate on transport of
705 arsenate through an oxisol. *Soil Science Society of America Journal* 59, 1289–1294.

706 Milivojevic, D.B., Nikolicand, B.R., Drinic, G., 2006. Effects of arsenic on phosphorus
707 content in different organs and chlorophyll fluorescence in primary leaves of soybean.
708 *Biologia Plantarum* 50, 149-151.

709 Mkandawire, M., Lyubun, Y.V., Kosterin, P.V., Dudel, E.G., 2004. Toxicity of arsenic
710 species to *Lemna gibba* L. and the influence of phosphate on arsenic bioavailability.
711 *Environmental Toxicology* 19, 26–34.

712 Macnair, M.R., Cumbes, Q., 1987. Evidence that arsenic resistance in *Holcus lanatus* L. is
713 caused by an altered phosphate uptake system. *New Phytologist* 107, 387-394.

714 Manning, B.A., Goldberg, S., 1996. Modeling competitive adsorption of As(V) with
715 phosphate and molybdate on oxide minerals. *Soil Science Society of America Journal* 60,
716 121-131.

717 Mojsilovic, O., McLaren, R.G., Condon, L.M., 2011. Modelling arsenic toxicity in wheat:
718 Simultaneous application of diffusive gradients in thin films to arsenic and phosphorus in
719 soil. *Environmental Pollution* 159 (10), 2996-3002.

720 Mwamila L, Gustafsson JP (2011) Arsenic (V) and phosphate sorption to Swedish clay soils -
721 Freundlich sorption modelling, KTH, Skolan för arkitektur och samhällsbyggnad (ABE),
722 Mark- och vattenteknik (flyttat 20130630), Miljögeokemi och ekoteknik.

723 Nagy, F., Karandashov, V., Chague, W. et al., 2005. The characterization of novel
724 mycorrhiza-specific phosphate transporters from *Lycopersicon esculentum* and *Solanum*
725 *tuberosum* uncovers functional redundancy in symbiotic phosphate transport in
726 solanaceous species. *Plant Journal* 42, 236–250.

727 Nussaume, L., Kanno, S., Javot, H., Marin, E., Pochon, N., Ayadi, A., Nakanishi, T.M.,
728 Thibaud, M.-C., 2011. Phosphate import in plants: focus on the PHT1 transporters.
729 *Frontiers in Plant Science* 2, 1-12.

730 O'Neill, 1992. Heavy metals in soils. Alloway, B.J (Ed.), 2nd Edition, Blackie Academic &
731 Professional, London, UK, pp. 105–121.

732 Onken BM, Adriano DC (1997) Arsenic availability in soil with time under saturated and
733 subsaturated conditions. *Soil Science Society of America Journal* 61, 746-751.

734 Paivoke, A.E.A., Simola, L.K., 2001. Arsenate toxicity to *Pisum sativum*: mineral nutrients,
735 chlorophyll content and phytase activity. *Ecotoxicology and Environmental Safety* 49,
736 111–121.

737 Pantsar-Kallio, M., Manninen, P.K.G., 1997. Speciation of mobile arsenic in soil samples as a
738 function of pH. *Science of the Total Environment* 204, 193–200.

739 Panuccio, M.R., Logoteta, B., Beone, G.M., Cagnin, M., Cacco, G., 2012. Arsenic uptake and
740 speciation and the effects of phosphate nutrition in hydroponically grown kikuyu grass
741 (*Pennisetum clandestinum* Hochst). *Environmental Science and Pollution Research* 19,
742 3046–3053.

743 Paszkowski, U., Kroken, S., Roux, C. et al. 2002. Rice phosphate transporters include an
744 evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis.
745 *Proceedings of National Academy of Science, USA* 99, 13324–13329.

746 Peryea, F. J., 1991. Phosphate-induced release of arsenic from soils contaminated with lead
747 arsenate. *Soil Science Society of America Journal* 55, 1301–1306.

748 Peryea, F.J., 1998. Phosphate starter fertilizer temporarily enhances soil arsenic uptake by
749 apple trees grown under field conditions. *Horticulture Science* 33, 826–829.

750 Pickering, I.J., George, M.J., Smith, R.D. et al., 2000. Reduction and coordination of arsenic
751 in Indian Mustard. *Plant Physiology* 122, 1171–1177.

752 Pigna, M., Cozzolino, V., Violante, A., Meharg, A.A., 2009. Influence of Phosphate on the
753 Arsenic Uptake by Wheat (*Triticum durum* L.) Irrigated with Arsenic Solutions at Three
754 Different Concentrations. *Water Air and Soil Pollution* 197, 371–380.

755 Pigna, M., Cozzolino, V., Caporale, A.G., Mora, M.L., Di Meo, V., Jara, A.A., et al., 2010.
756 Effects of phosphorus fertilization on arsenic uptake by wheat grown in polluted soils.
757 *Journal of Soil Science and Plant Nutrition* 10, 428–442.

758 Pigna, M., Caporale, A.G., Cozzolino, V., Fernández-López, C., Mora, M.L., Sommella, A.
759 Violante, A., 2012. Influence of phosphorus on the arsenic uptake by tomato(*Solanum*
760 *lycopersicum* L) irrigated with arsenic solutions at four different concentrations. *Journal of*
761 *Soil Science and Plant Nutrition* 12, 775-784.

762 Planas, D., Healey, F.P., 1978. Effects of arsenate on growth and phosphorus metabolism of
763 phytoplankton. *Journal of Phycology* 14, 337–341.

764 Pollard, A.J., Powell, K.D., Harper, F.A., Smith, J.A.C., 2002. The genetic basis of metal
765 hyperaccumulation in plants. *Critical Reviews in Plant Science* 21, 539–566.

766 Porter, E.K., Peterson, P.J., 1977. Arsenic resistance in grasses growing on mine waste.
767 *Environmental Pollution* 14, 255–265.

768 Pratas, J., Prasad, M.N.V., Freitas, H., Conde, L., 2005. Plants growing in abandoned mines
769 of Portugal are useful for biogeochemical exploration of arsenic, antimony, tungsten and
770 mine reclamation. *J Geochem Explor*, 85, 99-107.

771 Puckett, E.E., Serapiglia, M.J., DeLeon, A.M., Long, S., Minocha, R., Smart, L.B., 2012.
772 Differential expression of genes encoding phosphate transporters contributes to arsenic
773 resistance and accumulation in shrub willow (*Salix* spp.). *Environmental and Experimental*
774 *Botany* 75, 248– 257.

775 Qin, J., Rosen, B.P., Zhang, Y., Wang, G., Franke, S., Rensing, C., 2006. Arsenic
776 detoxification and evolution of trimethylarsine gas by a microbial arsenite S-
777 adenosylmethionine methyltransferase. *Proceedings of National Academy of Science, USA*
778 103, 2075-2080.

779 Quaghebeur, M., Rengel, Z., Smirk, M., 2003. Arsenic speciation in terrestrial plant material
780 using microwave-assisted extraction, ion chromatography and inductively coupled plasma
781 mass spectrometry. *Journal of Analytical and Atomic Spectrometry* 18, 128-34.

782 Quaghebeur, M., Rengel, Z., 2003. The distribution of As(V) and As(III) in shoots and roots
783 of *Holcus lanatus* is influenced by arsenic resistance and As(V) and phosphate supply.
784 *Plant Physiology* 132, 1600–1609.

785 Quaghebeur, M., Rengel, Z., 2004. Phosphate and As(V) interactions in the rhizosphere of
786 canola (*Brassica napus*). *Functional Plant Biology* 31, 1085–1094.

787 Quaghebeur, M., Rate, A., Rengel, Z., Hinz, C., 2005. Desorption kinetics of arsenate from
788 kaolinite as influenced by pH. *Journal of Environmental Quality* 34, 479-86.

789 Quaghebeur, M., Rengel, Z., 2005. Arsenic speciation governs arsenic uptake and transport in
790 terrestrial plants. *Microchimica Acta* 151, 141-52.

791 Raab, A., Feldmann, J., Meharg, A.A., 2004. The nature of arsenic-phytochelatin complexes
792 in *Holcus lanatus* and *Pteris cretica*. *Plant Physiology* 134, 1113–1122.

793 Rahman, M.A., Hasegawa, H., Rahman, M.M., Islam, M.N., Miah, M.A.M., Tasmien, A.,
794 2007. Effect of arsenic on photosynthesis, growth and yield of five widely cultivated rice
795 (*Oryza sativa* L.) varieties in Bangladesh. *Chemosphere* 67, 1072–1079.

796 Rahman, M.A., Hasegawa, H., Rahman, M.M., Miah, M.A.M., Tasmien, A., 2008.
797 Straighthead disease of rice (*Oryza sativa* L.) induced by arsenic toxicity. *Environmental*
798 *and Experimental Botany* 62, 54–59.

799 Rauf, MA, Hakim, MA, Hanafi, MM, Islam, MM, Rahman, GKMM, Panaullah, GM, 2011.
800 Bioaccumulation of arsenic (As) and phosphorous by transplanting Aman rice in arsenic-
801 contaminated clay soils. *Australian Journal of Crop Science* 5, 1678-1684.

802 Rausch, C., Bucher, M., 2002. Molecular mechanisms of phosphate transport in
803 plants. *Planta* 216, 23–37.

804 Reina, S.V., Esteban, E., Goldsbrough, P., 2005. Arsenate-induced phytochelatin in white
805 lupin: influence of phosphate status. *Physiologia Plantarum* 124, 41–49.

806 Remy, E., Cabrito, T.R., Batista, R.A., Teixeira, M.C., Sa-Correia, I., Duque, P., 2012. The
807 Pht1;9 and Pht1;8 transporters mediate inorganic phosphate acquisition by the *Arabidopsis*
808 *thaliana* root during phosphorus starvation. *New Phytologist* 195, 356–371.

809 Rose, T.J., Impa, S.M., Rose, M.T., Pariasca-Tanaka, J., Mori, A., Heuer, S., Johnson-
810 Beebout, S.E., Wissuwa, M., 2013. Enhancing phosphorus and zinc acquisition efficiency
811 in rice: a critical review of root traits and their potential utility in rice breeding. *Annals of*
812 *Botany* 112, 331–345.

813 Rouached, H., Arpat, A.B., Poirier, Y., 2010. Regulation of phosphate starvation responses in
814 plants: signaling players and cross-talks. *Molecular Plant* 3, 288–299.

815 Roy, W.R., Hassett, J.J., Griffin, R.A., 1986. Competitive interactions of phosphate and
816 molybdate on arsenate adsorption. *Soil Science* 142, 203–210.

817 Rumberg, C.B., Engel, R.E., Meggitt, W.F., 1960. Effect of phosphorus concentration on the
818 absorption of arsenate by oats from nutrient solution. *Agronomy Journal* 52, 452–453.

819 Salmon, S.U., Rate, A.W., Rengel, Z., Appleyard, S., Prommer, H., Hinz, C., 2014. Reactive
820 transport controls on sandy acid sulfate soils and impacts on shallow groundwater quality.
821 *Water Resources Research* 50, 4924-4952.

822 Sanchary, I.J., Huq, S.M.I., 2017. Remediation of arsenic toxicity in the soil-plant system by
823 using zinc fertilizers. *Journal of Agricultural Chemistry and Environment* 6, 30-37.

824 Santos, J.A.G., Gonzaga, M.I.S., Ma, L.Q., Srivastava, M., 2008. Timing of phosphate
825 application affects arsenic phytoextraction by *Pteris vittata* L. of different ages.
826 *Environmental Pollution* 154, 306-311.

827 Schachtman, D.P., Reid, R.J., Ayling, S.M., 1998. Phosphorus uptake by plants: from soil to
828 cell. *Plant Physiology* 116, 447–453.

829 Schunmann, P.D., Richardson, A.D., Vickers, C.E., Delhaize, E., 2004a. Promoter analysis of
830 the barley Pht1;1 phosphate transporter gene identifies regions controlling root expression
831 and responsiveness to phosphate deprivation. *Plant Physiology* 136, 4205–4214.

832 Schunmann, P.D., Richardson, A.D., Smith, F.W., Delhaize, E., 2004b. Characterization of
833 promoter expression patterns derived from the Pht1 phosphate transporter genes of barley
834 (*Hordeum vulgare* L.). *Journal of Experimental Botany* 55, 855–865.

835 Shaibur, M.R., Adjadeh, T.A., Kawai, S., 2013. Effect of phosphorus on the concentrations of
836 arsenic, iron and some other elements in barley grown hydroponically. *Journal of Soil*
837 *Science and Plant Nutrition* 13, 87-98.

838 Sharma, S., Anand, G., Singh, N., Kapoor, R., 2017. Arbuscular Mycorrhiza augments arsenic
839 tolerance in wheat (*Triticum aestivum* L.) by strengthening antioxidant defense system and
840 thiol metabolism. *Frontiers in Plant Science* 8, 906.

841 Sharples, J.M., Meharg, A.A., Chambers, S.M., Cairney, J.W.G., 1999. Arsenate sensitivity in
842 ericoid and ectomycorrhizal fungi. *Environmental Toxicology and Chemistry* 18, 1848–
843 1855.

844 Sharples, J.M., Meharg, A.A., Chambers, S.M., Cairney, J.W.G., 2000a. The symbiotic
845 solution to arsenic contamination. *Nature* 404, 951–952.

846 Sharples, J.M., Meharg, A.A., Chambers, S.M., Cairney, J.W.G., 2000b. Mechanism of
847 arsenate resistance in the ericoid mycorrhizal fungus *Hymenoscyphus ericae*. *Plant*
848 *Physiology* 124, 1327–1334.

849 Shetty, K.G., Hetrick, B.A.D., Schwab, A.P., 1995. Effects of mycorrhizae and fertilizer
850 amendments on zinc resistance of plants. *Environmental Pollution* 88, 307–314.

851 Shin, H., Shin, H.S., Dewbre, G.R., Harrison, M.J., 2004. Phosphate transport in *Arabidopsis*:
852 *Pht1;1* and *Pht1;4* play a major role in phosphate acquisition from both low- and high-
853 phosphate environments. *Plant Journal* 39, 629–642.

854 Singh, N., Ma, L.Q., 2006. Arsenic speciation, and arsenic and phosphate distribution in
855 arsenic hyperaccumulator *Pteris vittata* L. and non-hyperaccumulator *Pteris ensiformis* L.
856 *Environmental Pollution* 141, 238-246.

857 Shoji, R., Yajima, R., Yano, Y., 2008. Arsenic speciation for the phytoremediation by the
858 Chinese brake fern, *Pteris vittata*. *Journal of Environmental Science* 20, 1463–1468.

859 Smith, E., Naidu, R., Alston, A.M., 1998. Arsenic in the soil environment: A review.
860 *Advances in Agronomy* 64, 149–195.

861 Smith, E., Naidu, R., Alston, A.M., 2002. Chemistry of inorganic arsenic in soils. II. Effect of
862 phosphorus, sodium, and calcium on arsenic absorption. *Journal of Environmental Quality*
863 31, 557–563.

864 Smith, S.E., Smith, F.A., Jakobsen, I., 2003. Mycorrhizal fungi can dominate phosphate
865 supply to plants irrespective of growth responses. *Plant Physiology* 133, 16–20.

866 Smith, S.E., Smith, F.A., Jakobsen, I., 2004. Functional diversity in arbuscular mycorrhizal
867 (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated
868 with mycorrhizal responses in growth or total P uptake. *New Phytologist* 162, 511–524.

869 Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis. Academic Press, New York, London,
870 Burlington, San Diego.

871 Smith, S.E., Christophersen, H.M., Pope, S., Smith, F.A., 2010. Arsenic uptake and toxicity in
872 plants: integrating mycorrhizal influences. *Plant and Soil* 327, 1–21.

873 Sneller, E.F.C., Van Heerwaarden, L.M., Kraaijeveld-Smit, F.J.L., Ten Bookum, W.M.,
874 Koevoets, P.L.M., Schat, H, et al., 1999. Toxicity of As(V) in *Silene vulgaris*,
875 accumulation and degradation of As(V) induced phytochelatins. *New Phytologist* 44, 223–
876 232.

877 Srivastava, M., Santos, J., Srivastava, P., Ma, L.Q., 2010. Comparison of arsenic
878 accumulation in 18 fern species and four *Pteris vittata* accessions. *Bioresource Technology*
879 101, 2691–2699.

880 Szegedi, K., Vetterlein, D., Jahn, R., 2010. Modelling rhizosphere transport in the presence of
881 goethite, including competitive uptake of phosphate and As(V). *Plant and Soil* 330, 481-
882 501.

883 Tao, Y., Zhang, S., Jian, W., Yuan, C., Shan, X.-Q., 2006. Effects of oxalate and phosphate
884 on the release of arsenic from contaminated soils and arsenic accumulation in wheat.
885 *Chemosphere* 65, 1281–1287.

886 Talukder, A.S.M.H.M., Meisner, C.A., Sarkar, M.A.R., Islam, M.S., 2011. Effect of water
887 management, till age options and phosphorus status on arsenic uptake in rice.
888 *Ecotoxicology and Environmental Safety* 74, 834–839.

889 Talukder, A.S.M.H.M., Meisner, C.A., Sarkar, M.A.R., Islam, M.S., Sayre, K.D., Duxbury,
890 J.M., Lauren, J.G., 2012. Effect of water management, arsenic and phosphorus levels on
891 rice in a high-arsenic soil–water system: II. Arsenic uptake. *Ecotoxicology and*
892 *Environmental Safety* 80, 145-151.

893 Taylor, G.J., Crowder, A.A., Rodden, R., 1984. Formation and morphology of iron plaque on
894 the roots of *Typha latifolia* L. growing in solution culture. *American Journal of Botany* 71,
895 666–1675.

896 Tu, S., Ma, L.Q., 2003a. Effects of As(V) and phosphate on their accumulation by an arsenic-
897 hyperaccumulator *Pteris vittata* L. *Plant and Soil* 249, 373–382.

898 Tu, S., Ma, L.Q., 2003b. Interactive effects of pH, arsenic and phosphorus on uptake of As
899 and P and growth of the arsenic hyperaccumulator *Pteris vittata* L. under hydroponic
900 conditions. *Environmental and Experimental Botany* 50, 243-251.

901 Tu, S., Ma, L.Q., MacDonald, G.E., Bondada, B., 2004. Effects of arsenic species and
902 phosphorus on arsenic absorption, As(V) reduction and thiol formation in excised parts of
903 *Pteris vittata* L. *Environmental and Experimental Botany* 51, 121–131.

904 Tuan, L.Q., Huong, T.T.T., Hong, P.T.A., Kawakami, T., Shimanouchi, T., Umakoshi, H.,
905 Kuboi, R., 2008. Arsenic (V) induces a fluidization of algal cell and liposome membranes.
906 *Toxicology In Vitro* 22, 1632–1638.

907 Turnau, K., Kottke, I., Oberwinkler, F., 1993. Element localization in mycorrhizal roots of
908 *Pteridium aquilinum* (L.) collected from experimental plots treated with cadmium dust.
909 *New Phytologist* 123, 313–324.

910 Ullrich-Eberius, C.I., Sanz, A., Novacky, A.J., 1989. Evaluation of arsenate- and vanadate-
911 associated changes of electrical membrane potential and phosphate transport in *Lemna*
912 *gibba* L. *Journal of Experimental Botany* 40:119–128.

913 Ultra Jr., V.U., Tanaka, S., Sakurai, K., Iwasaki, K., 2007. Effects of arbuscular mycorrhiza
914 and phosphorus application on arsenic toxicity in sunflower (*Helianthus annuus* L.) and on
915 the transformation of arsenic in the rhizosphere. *Plant and Soil* 290, 29–41.

916 Vetterlein, D., Szegedi, K., Ackermann, J., Mattusch, J., Neue, H.-U., Tanneberg, H., Jahn R.,
917 2007. Competitive mobilization of phosphate and As(V) associated with goethite by root
918 activity. *Journal of Environmental Quality* 36, 1811–1820.

919 Vetterlein, D., Jahn, R., Mattusch, J., 2009. Comparison of corn and lupin in respect to As
920 mobilisation, uptake and release in an arsenic contaminated floodplain soil. *Proceeding of*
921 *Internatiol Plant Nutrition Colloquim XVI*, 2009.

922 Violante, A., Pigna, M., 2002. Competitive sorption of As(V) and phosphate on different clay
923 minerals and soils. *Soil Science Society of America Journal* 66, 1788–1796.

924 Walsh, L., Keeney, D., 1975. Behavior and phytotoxicity of inorganic arsenicals in soils. In:
925 EA Woolson (ed) *Arsenical Pesticides*, ACS Symposium Series 7, American Chemical
926 Society. Washington, DC.

927 Wang, J., Zha, F.-J., Meharg, A.A., Raab, A., Feldmann, J., McGrath, S.P., 2002.
928 Mechanisms of arsenic hyperaccumulation in *Pteris vittata*. Uptake kinetics, interactions
929 with phosphate, and arsenic speciation. *Plant Physiology* 130, 1552–1561.

930 Wang G, Kennedy SP, Fasiludeen S, Rensing C, DasSarma S (2004) Arsenic resistance
931 in *Halobacterium* sp. strain NRC-1 examined by using an improved gene knockout
932 system. *Journal of Bacteriology* 186, 3187-3194.

933 Wenzel, W.W., Brandstetter, A., Wutte, H., Lombi, E., Prohaska, T., Stingeder, G., Adriano,
934 D.C., 2002. Arsenic in field-collected soil solutions and extracts of contaminated soils and
935 its implication to soil standards. *Journal of Plant Nutrition and Soil Science* 165, 221-228.

936 Woolson, E.A., 1973. Arsenic phytotoxicity and uptake in six vegetable crops. *Weed Science*
937 21, 524–527.

938 Xia, Y.-S., Chen, B.-D., Christie, P., Smith, F.A., Wang, Y.S., Li, X.-L., 2007. Arsenic uptake
939 by arbuscular mycorrhizal maize (*Zea mays* L.) grown in an arsenic-contaminated soil with
940 added phosphorus. *Journal of Environmental Science* 19, 1245–1251.

941 Xiong J, Wu L, Tu S, Van Nostrand JD, He Z, Zhou J, Wang G (2010) Microbial
942 communities and functional genes associated with soil arsenic contamination and the
943 rhizosphere of the arsenic-hyperaccumulating plant *Pteris vittata* L. *Applied and*
944 *Environmental Microbiology* 76, 7277–7284.

945 Xu, P.L., Christie, P., Liu, Y., Zhang, J.L., Li, X.L., 2008. The arbuscular mycorrhizal fungus
946 *Glomus mosseae* can enhance arsenic resistance in *Medicago truncatula* by increasing
947 plant phosphorus status and restricting arsenate uptake. *Environmental Pollution* 156, 215-
948 220.

949 Yan, X., Zhang, M., Liao, X., Tu, S., 2012. Influence of amendments on soil arsenic
950 fractionation and phytoavailability by *Pteris vittata* L. *Chemosphere* 88, 240–244.

951 Ye, W.-L., Khan, M. A., McGrath, S.P., Zhao, F.-J., 2011. Phytoremediation of arsenic
952 contaminated paddy soils with *Pteris vittata* markedly reduces arsenic uptake by rice.
953 *Environmental Pollution* 159, 3739-3743.

954 Zhao, F.J., Ma, J.F., Meharg, A.A., McGrath, S.P. 2009. Arsenic uptake and metabolism in
955 plants. *New Phytologist* 181, 777-794.

956 Zhu, Y.-G., Smith, F.A., Smith, S.E., 2003. Phosphorus efficiencies and responses of barley
957 (*Hordeum vulgare* L.) to arbuscular mycorrhizal fungi grown in highly calcareous soil.
958 *Mycorrhiza* 13, 93–100.

959 Zhu, Y.-G., Geng, C.-N., Tong, Y.-P., Smith, S.E., Smith, F.A., 2006. Phosphate (Pi) and
960 As(V) uptake by two wheat (*Triticum aestivum*) cultivars and their doubled Haploid Lines.
961 *Annals of Botany* 98, 631–636.

962 Zou Q, Liu F, Yang J-H (2009) Adsorption-desorption and competitive adsorption of arsenic
963 and phosphorus in purple soil. *Journal of Applied Ecology* 20, 1383-1389.

964 Zupancic, M., Lavrič, S., Bukovec, P., 2012. Metal immobilization and phosphorus leaching
965 after stabilization of pyrite ash contaminated soil by phosphate amendments. *Journal of*
966 *Environmental Monitoring* 14, 704–710.

967

968

Figure captions

969

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

973

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

977

978 **Fig. 3.** Role of AM in modifying As-Pi interactions, and As and Pi uptake by plant root. The
979 arbuscular mycorrhizal (AM) symbioses increase Pi uptake by plant roots and Pi/As ratio in
980 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	<i>Zea mays</i>	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	<i>Zea mays</i>	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	<i>Pteris vittata</i>	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	<i>Oryza sativa</i>	Pi	Increasing shoot Pi for breeding rice with low grain As	Lu et al. (2010)
Soil	<i>Oryza sativa</i>	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	<i>T. durum</i>	Pi (75 kg/ha)	Prevented As uptake and translocation in plants	Pigna et al. (2010)
Soil	<i>H. vulgare</i>	Pi/ As	Pi strongly inhibited As(V) uptake. As weakly inhibited Pi uptake	Asher and Reay(1979)
Soil-sand, soil	<i>H. vulgare</i> <i>T. vulgare</i>	Pi (20-120 mg/kg)	Increased As uptake; decreased As(V) toxicity not by lowering As uptake, but by enhancing Pi nutrition. No competition between As and Pi.	Christophersen et al. (2009a), Tao et al. (2006)
Soil	<i>C. arietinum</i>	Pi (50-400)	Pi increased As uptake, but partially protected membranes from damage	Gunes et al. (2009)
Soil	<i>L. cinereus</i>	As/Pi	High level of As and low Pi supply decreased plant growth	Knudson et al. (2003)
Loam soil	<i>P. armeniaca</i>	Pi	Increased shoot and root As in soil contaminated with Pb-arsenate pesticide residue.	Creger & Peryea (1994)
Soil	<i>Arabidopsis thaliana</i>	Pi (10-40 mg/kg)	Low Pi supply increased As uptake and plant growth. High Pi supply decreased As uptake due to competition on surface of soil particles and plant roots.	Geng et al. (2005)
Soil	<i>Solanum lycopersicum</i>	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	<i>H. lanatus</i>	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(III) 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 for carrot, 2.5–10 for 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
<i>Pteris vittata</i>	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)
<i>Oryza sativa</i>	Pi, 0.1 mM	High Pi concentration decreased As uptake; high As concentration slightly decreased Pi uptake	Lihong and Guilan (2009)
<i>Holcus lanatus</i>	Pi	Decreased As(V) uptake in nonresistant, but less in resistant plants	Meharg & MacNair (1992)
<i>Lemna gibba</i>	Pi, 40 mg/L	High Pi reduced As(V, III) uptake; high As reduced Pi uptake	Mkandawire et al. (2004)
<i>M. sativa</i>	Pi	Strongly suppressed As uptake	Khattak et al. (1991)
<i>Silene vulgaris</i>	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)
<i>Avena sativa</i>	Pi	Decreased As(V) uptake, but little effect on As(III) uptake.	Rumberg et al. (1960)
<i>Glycine max</i>	As, 32-96 μ M	Decreased Pi content in soybean organs	Milivojevic et al. (2006)
<i>T. aestivum</i>	Pi	High-affinity uptake system switched on at 25 mM Pi.	Zhu et al. (2006)

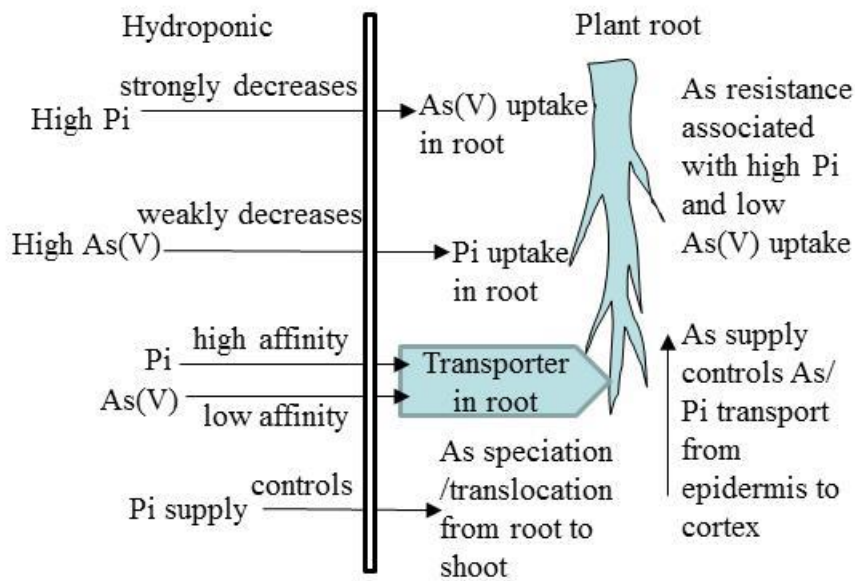


Fig. 1. As-Pi interactions and uptake by plants in hydroponics. As and Pi supply variably control As and Pi uptake by plant roots. Pi supply strongly decreases As uptake, while As supply weakly decreases Pi uptake. Pi has higher affinity for plant roots than As.

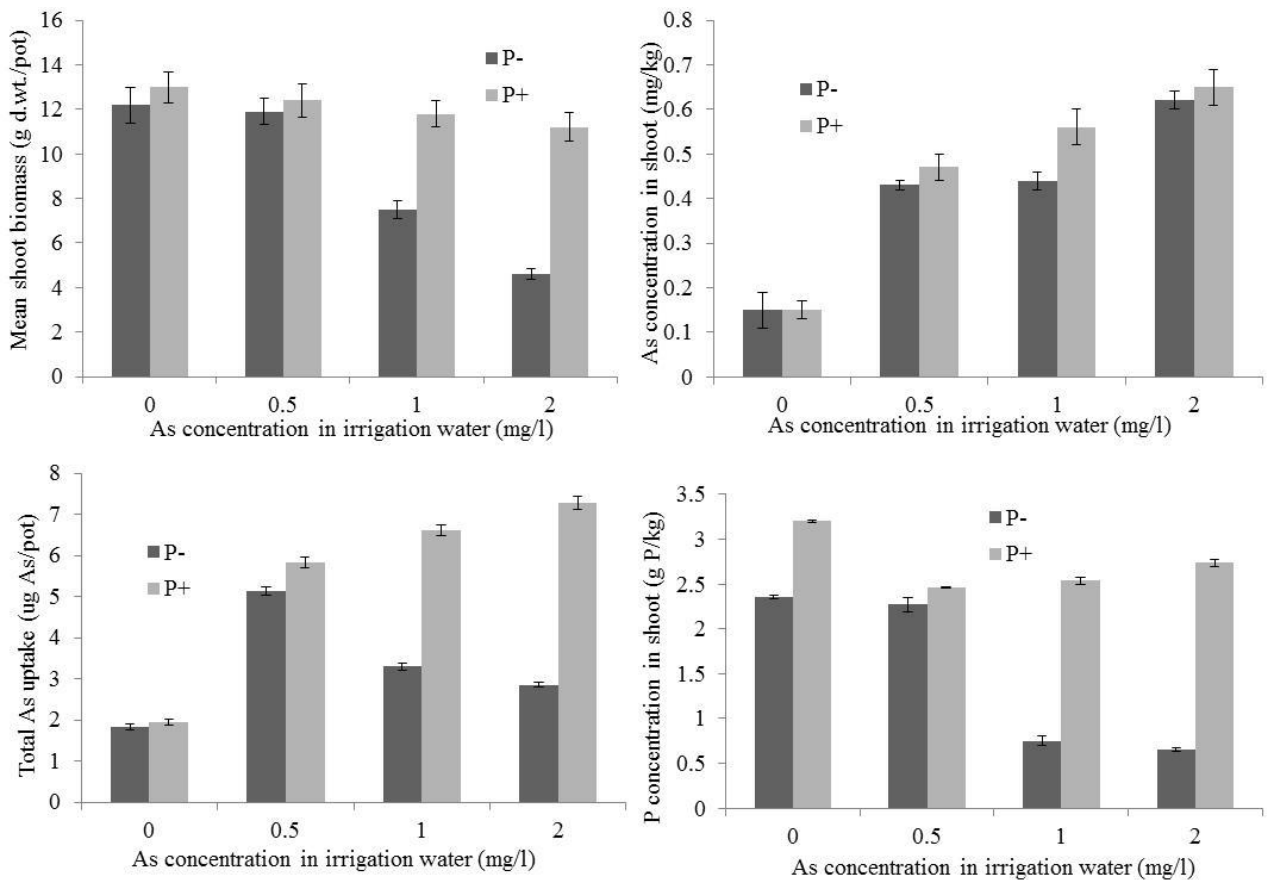


Fig. 2. Mean shoot biomass, As and Pi concentrations in shoots and total As uptake by wheat plants grown in soil irrigated with As containing water at three concentrations amended and non-amended with Pi (data analysis from Pigna et al., 2009).

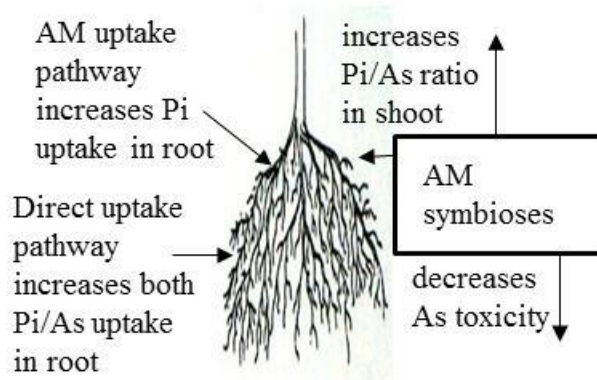


Fig. 3. Role of AM in modifying As-Pi interactions, and As and Pi uptake by plant root. The arbuscular mycorrhizal (AM) symbioses increase Pi uptake by plant roots and Pi/As ratio in shoot, while they decrease As uptake by roots.