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Review

Mechanism of arsenic uptake, translocation and plant resistance to accumulate arsenic in rice grains

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ABSTRACT

A global data analysis shows that rice grain arsenic (As) concentrations increase with increasing soil As concentrations until about 60 mg As kg^{-1}soil and then decreases. Of the total grain As, 54% is composed of inorganic As. Therefore, when considering the WHO-permissible grain inorganic As concentration, i.e. 0.2 mg As kg^{-1}, the permissible grain total As concentrations is 0.37 mg total As kg^{-1}grain. Soil total As concentration when grain total As concentration reaches permissible level is 5.5 mg As kg^{-1}soil. Therefore, the suitable soil As concentrations for screening rice cultivars in rice agroecosystems for As resistance is 5–60 mg As kg^{-1}soil. Rice has traits to reduce uptake and translocation of As to grains. Cultivars with higher root porosity, radial oxygen loss, or formation of iron plaques bind more As to iron plaques, reducing As uptake (i.e. As avoidance). Once taken up, glutathione/glutaredoxin-mediated As reduction, and phytochelatin-dependent complexation and sequestration in vacuoles result in less translocation of As to the grain. Moreover, generation of reactive oxygen species and the production of antioxidant enzymes further reduce As toxicity (i.e. As resistance). These resistance mechanisms in rice agroecosystems are further enhanced when adequate concentrations of silicon and sulfur are present in soils and tissues, and when plants are associated with arbuscular mycorrhizal fungi, particularly under aerobic or intermittent-aerobic soil condition. Therefore, As concentrations in rice ecosystems decrease in the order of: roots > leaves > grains, and in grains: hull > bran polish > brown rice > raw rice > polished rice > cooked rice. Within the grain, As speciation is affected by the location in the grain, forms of As species, the grain-filling stage, geographic origin, ecosystem management and cultivars used. Indica type accumulates more As in their grains than japonica type. Rice grain production, within safe limits of As, requires the consideration of soil As dynamics including soil management, cultivar responses including uptake and translocation, and post-harvest processing techniques.

1. Introduction

Human exposure to arsenic (As) results from several pathways such as drinking water, food, beverages, soil, inhalation of dust and atmospheric particulates (Bhattacharyya et al., 2003; Kapaj et al., 2006; Kar et al., 2006; Nriagu et al., 2007; Nath et al., 2008; Naidu and Bhattacharya, 2009; Chatterjee et al., 2010). However, consumption of rice is the primary source of As for humans in a non-seafood diet, especially in the tropics (Lee et al., 2008; Torres-Escribano et al., 2008; Halder et al., 2014). In populations not suffering from elevated As in drinking water, chronic exposure to inorganic As may also occur through the consumption of As-contaminated rice including baby food containing rice (Williams et al., 2007; Lee et al., 2008; Meharg et al., 2008; Halder et al., 2014; Lai et al., 2015; Signes-Pastor et al., 2016a). The average daily consumption of rice by an Asian adult varies in the range of 200–600 g, depending on the region (Duxbury et al., 2003; Rahman et al., 2008; Zavala and Duxbury, 2008; Zhu et al., 2008; Garnier et al., 2010), and in Ghana in Africa it is 32–232 g (Adomako et al., 2011). Due to this variation in rice intake and in the concentration of As in rice, the potential daily intake values of As by an adult is also highly variable among studies and regions, e.g., 19.6 μg in India (Kumar et al., 2016), 100–350 μg in Bangladesh (Rahman et al., 2008; Panaullah et al., 2008), and 69 μg in Cambodia (Phan et al., 2014). Some of these estimates are much higher than the approximate As intake through drinking water of 2 L per day at the acceptable WHO limit of 10 μg L^{-1} inorganic As. It has also been reported from the Bengal delta, India that daily dietary intake of inorganic As by an adult from rice is 2.32 μg As kg^{-1} body wt. day^{-1} and this is more than the

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WHO recommended potential daily intake value of 2.1 μg As kg^{-1} body wt. day^{-1} (Roychowdhury, 2008). Moreover, daily total As intake per body weight reported for Cambodia was 1.46 μg kg^{-1} body wt. day^{-1} (Phan et al., 2014). Similarly, daily total As intake of 0.002, 0.184 μg kg^{-1} body wt. day^{-1} in France (Jitaru et al., 2016), and 0.34, 0.49 μg kg^{-1} body wt. day^{-1} in China for children and adults, respectively have also been reported (Huang et al., 2013).

Carbonell-Barrachina et al. (2012) analysed the inorganic As concentration in food items for infants available in the markets of Spain which were mainly manufactured in China, and found that approximately 23% of the pure infant rice samples showed inorganic As concentrations over 150 μg kg^{-1} (i.e. Chinese limit- USDA, 2006). When daily intake of inorganic As by infants (4–12 months) was estimated and expressed on a body-weight basis (μg d^{-1} kg^{-1} body wt.), it was higher for all infants aged 8–12 months than drinking water maximum exposures predicted for adults (10 μg L^{-1} standard), indicating the infants are at a higher risk of As toxicity than adults. Similarly, elevated inorganic and total As concentrations in rice and rice-based infant food were reported through market surveys conducted in Australia, Finland, Kingdom of Saudi Arabia, Sweden and United Kingdom (Meharg et al., 2008; Ljung et al., 2011; Rintala et al., 2014; Shraim, 2017). Epidemiological studies show that chronic As poisoning can cause serious health effects including cancers, melanosis (hyper-pigmentation or dark spots and hypo-pigmentation or white spots), hyper-keratosis (skin hardening), restrictive lung disease, peripheral vascular disease (black foot disease), gangrene, diabetes mellitus, hypertension and ischemic heart disease (Mandal and Suzuki, 2002; Chatterjee et al., 2010; Maity et al., 2012). Because of these health risks associated with As, it is important to study the dynamics of As in soil and rice plants including grains aimed at reducing As accumulation in soil, uptake by rice plants and translocation to rice grains. Due to the risks associated with As in rice grain, the maximum acceptable total As level in rice grains was 1 mg total As kg^{-1} grain (Sauvé, 2014). This level was based on previous risk assessments across a wide range of food products. However, several recent studies on the levels of As in rice and rice-based products have provided sufficient evidence and data to question this overly generous threshold, specifically with regards to rice. Therefore, this limit was recently revised to 0.2 mg inorganic As kg^{-1} grain (WHO, 2016).

Soil and grain As concentrations reported in this review cannot be generalised as average or representative values for geographic regions. They should be considered as upper limits that can be expected at As-contaminated sites, as most of the experiments were conducted in fields with high concentrations of As, or soils used to conduct pot experiments were selected from areas with inherently high soil As concentrations or contaminated with As to test specific hypotheses (Table S1). A similar caution pertains to the data on daily As intake by humans in different regions. Moreover, as presented in Table S1, to date, there is an abundant amount of literature on 'As dynamics in rice' including As translocation and speciation in rice plants, and molecular and biochemical responses of rice to As toxicity generated through experiments conducted with variable complexities from simple hydroponic experiments to field and market surveys across the globe.

2. As uptake by rice

The uptake of As by rice from soil strongly depends on the quantities and speciation of As in the rhizosphere (Marin et al., 1992, 1993). Under conditions of submerged rice cultivation in anaerobic soil, arsenate (As(V)) is reduced to arsenite (As(III)) in the soil solid phase, followed by desorption of the latter from soil minerals due to its lower sorption capacity as compared with As(V) (Yamaguchi et al., 2014). Arsenite is taken up through a subclass of aquaporins (nodulin 26-like intrinsic proteins: NIPs), and then enters the stele through the silicon-(Si) uptake pathway (Ma et al., 2008; Panda et al., 2010). Among these proteins, some members are Si transporters that load As(III) into the xylem or secrete As(III) from the roots (Zhao et al., 2010). The NIP gene family consists of 10–13 genes in rice (Forrest and Bhave, 2007) which can be subdivided into three groups, NIP I, II and III on the basis of their selectivity (Ma et al., 2008; Zhao et al., 2010). Aquaporin *Lsi1* transports As(III) (Bienert et al., 2008; Ma et al., 2008), and also mediates silicic acid influx. It is expressed outer side of the plasma membranes of the exodermis and endodermis cells where Casparian strips are formed. Arsenite is an uncharged molecule with a diameter of approximately 411 pm (Ma et al., 2008), similar to silicic acid, and can be taken up by transporters of silicic acid, but not by aquaporins in general. Another silicic acid transporter also transporting As(III), *Lsi2*, is expressed at the inner side of the plasma membranes of the exodermis and endodermis cells, releasing As(III) into the cortex and into the stele (Ma et al., 2008). In the cytosol, As(III) reacts with sulfhydryl groups of proteins, affecting many biochemical functions (Tripathi et al., 2012; Kumar et al., 2015). Within the cell, As(III) can be detoxified via a reaction with phytochelatins, which results in As(III)–phytochelatin complexes that are ultimately sequestered in vacuoles (Briat, 2010). The transport of that complex across the tonoplast is believed to be mediated by a C-type ATP-binding cassette (ABC) transporter (Song et al., 2010, 2014), which may therefore be of paramount importance for As resistance in plants (Briat, 2010; Sanglard et al., 2016). Arsenite uptake follows Michaelis-Menten kinetics, with a K_m in the range of 3.7-22.9 μM As(III) (Abedin et al., 2002; Chen et al., 2005).

Among different forms of As in soil, As(V) is the predominant phytoavailable form in aerobic soils; like phosphate, it strongly sorbs onto mineral soil components (e.g., iron (hydr)oxides) (Takahashi et al., 2004). It is an analogue of phosphate and taken up by the high-affinity phosphate uptake system (Ullrich-Eberius et al., 1989; Meharg and Macnair, 1990; Zhao et al., 2010), and believed to be loaded into xylem vessels by phosphate transporter (PHT) proteins (Zhao et al., 2010; Wu et al., 2011). Recently, Begum et al. (2016) showed that As stress causes a consistent decrease in tissue P concentration and expression of phosphate transporters (*OsPT8*, *OsPT4*, *OsPHO1;2*) under both high and low P supply to rice cultivar BRRI 33. Moreover, a simultaneous increase in phytochelatin synthase (*OsPCS1*) expression and phytochelatin concentration in rice roots were also observed under As exposure. Overall, the results suggests that As stress down-regulates phosphate transporters, and enhances phytochelatin-mediated As sequestration to vacuoles in root cells, limiting As translocation to shoots.

The organic species, dimethyl-arsenic acid (DMA) and monomethyl-arsenic acid (MMA), are taken up at a much slower rate by the root than inorganic As, due to the lower affinity of transporters for organic As (Abedin et al., 2002; Raab et al., 2007; Abbas and Meharg, 2008). MMA uptake is also partly mediated by the silicic acid transporter *Lsi1*, while the specific transport pathways of DMA is not yet clear (Li et al., 2009; Carey et al., 2011). It was previously thought that plants are able to methylate As to produce various forms of organic As (Nissen and Benson, 1982; Wu et al., 2002), but recent studies have cast doubt on this. Plants such as rice appear to lack the ability to methylate As, but instead take up methylated As from the soil (Jia et al., 2013; Lomax et al., 2012; Zhao et al., 2013). The magnitude of As uptake by rice varies in the order of As(III) > As(V) > DMA > MMA (Raab et al., 2007; Finnegan and Chen, 2012). This is further affected by soil and crop management strategies, and the activity of microorganisms, as we will discuss below.

3. Translocation of As

3.1. Translocation of As from root to shoot

All major forms of inorganic (i.e. As(III) and As(V)) and organic (i.e. MMA and DMA) As can be translocated from roots to shoots via the xylem. Based on xylem sap analysis, Seyfferth et al. (2011) concluded that oxidised As species are dominant in the xylem (86% as As(V) and 14% as DMA), whereas reduced species (71% as As(III), 29% as As tris-