Environmental and Experimental Botany 132 (2016) 42–52

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Review

Arsenic toxicity in plants: Cellular and molecular mechanisms of its transport and metabolism

Muhammad A. Farooq[a], Faisal Islam[a], Basharat Ali[a,b], Ullah Najeeb[c], Bizeng Mao[d], Rafaqat A. Gill[a,d], Guijun Yan[e,f], Kadambot H.M. Siddique[f], Weijun Zhou[a,*]

[a] Institute of Crop Science and Zhejiang Key Laboratory of Crop Germplasm, Zhejiang University, Hangzhou 310058, China
[b] Institute of Crop Science and Resource Conservation, University of Bonn, Bonn 53115, Germany
[c] Plant Breeding Institute, Faculty of Agriculture and Environment, The University of Sydney, NSW 2015, Australia
[d] Institute of Biotechnology and State Key Laboratory for Rice Biology, Zhejiang University, Hangzhou 310058, China
[e] School of Plant Biology, Faculty of Science, The University of Western Australia, LB 5005 Perth, WA 6001, Australia
[f] The UWA Institute of Agriculture, The University of Western Australia, LB 5005 Perth, WA 6001, Australia

ARTICLE INFO

Article history:
Received 17 June 2016
Received in revised form 11 August 2016
Accepted 11 August 2016
Available online 13 August 2016

Keywords:
Arsenic
Bioavailability
Speciation
Transport
Metabolism
Toxicity
Mitigation

ABSTRACT

Arsenic (As), a naturally-occurring metalloid, is not essential for plant growth, but it can accumulate in plants to toxic levels. As a result, it can enter the food chain and pose health risk to humans. Multiple mechanisms are involved in the uptake and metabolism of As in plants. The most toxic forms of this element are As^{III} and As^{V}. Methylated As and arsenite (as As^{III}) move through the noduline 26-like intrinsic protein (NIP) aquaporin channels while arsenate (as As^{V}) is taken up through the phosphate transporters. In the Pteridaceae family, some fern species show hyper-accumulating behavior towards As in aboveground tissues. However, generally in plants, the chelation phenomenon detoxifies arsenite through complexation with the thiol-rich peptide. This comprehensive review encompasses the mechanisms of transport, metabolism, and tolerance that plants show in response to As. Some recent advancement in plant breeding, genetic modifications and remediation approaches to overcome soil and food contamination problems are also summarized. We will also evaluate the implications of these new findings and assess how this may help in developing the crops that can be grown in high As regions and ultimately will be safe for consumers.

Contents

---

[*] Corresponding author.
E-mail address: wjzhou@zju.edu.cn (W. Zhou).

http://dx.doi.org/10.1016/j.envexpbot.2016.08.004

1. Introduction

Arsenic is the 20th most ubiquitous element in the environment with an estimated concentration in the Earth's crust ranging from 1.5–3 mg kg^{-1} (Zhao et al., 2010; Drewniak and Sklodowska, 2013). In nature, more than 200 As-containing minerals have been found (Hoang et al., 2010); the most frequent As ore minerals are As sulfides such as realgar (As_4S_4), arsenopyrite (FeAsS) and orpiment (As_2S_3). Concentrations of As in the environment increases through both point and diffuse sources that may be natural (volcanic emissions, rock weathering, and discharge from hot springs) or anthropogenic activities (smelting, and use the of arsenicals as pesticides and herbicides, mining processes and wood preservatives). The background concentration of As in the soil ranges from 0.1–40 mg kg^{-1} and significantly differs among geographic regions. In European topsoil, the average concentration of As is about 7.0 mg kg^{-1} (Stafilov et al., 2010), but the estimated level in As-enriched metallogenic zones in south-western Poland was 18,100 mg kg^{-1} (Karczewska et al., 2007). In fresh water, As concentrations range from 0.15–0.45-μg L^{-1} depending on the source, availability, and geochemistry of the catchments (Bissen and Frimmel, 2003a,b) while those in seawater are usually less than 2 μg L^{-1} (Ng, 2005). Table 1 summarizes As contamination in soil and groundwater in different parts of the world.

Arsenic is classified as a class-1 carcinogen by the International Agency of Research on Cancer (IARC) that exhibits toxic effects depending on the type of exposure. The U.S. Environmental Protection Agency (EPA) and World Health Organization (WHO) state that the threshold level of As in drinking water is (10 μg L^{-1}). High concentration of As in drinking water, especially in South Asia, are a potential health hazard (Brammer and Ravenscroft, 2009; Nordstrom, 2002) with serious toxicological concerns for human health. Contamination of As is not limited to water sources. Soil contamination with As has become a serious environmental hazard, particularly in agricultural areas (Mishra et al., 2014). Arsenic accumulates in edible plant parts after being taken up from the soil, and is then consumed by humans (Finnegan and Chen, 2012). Rice cultivation is one such example of china where in mine-affected areas of the Hunan province, rice grains contained up to 723 μg g^{-1} of As, exceeding the Chinese maximum-allowed contaminant level of 150 μg g^{-1} for inorganic As (Okkenhaug et al., 2012; Williams et al., 2009). In Bangladesh and the United States, agricultural soils are contaminated with three-fold more As than the baseline (Panda et al., 2010). There is an urgent need to understand the mechanisms of assimilation and metabolism of As in crop plants and to develop the methods to mitigate its uptake and accumulation in plants. Therefore, a detailed understanding of biogeochemical aspects of As regarding its bioavailability, transport and uptake mechanisms and the potential mitigation approaches is important for developing appropriate techniques to reduce As uptake and accumulation in plants.

2. Bioavailability of arsenic

An important understanding about the risk related to As toxicity is its availability in term of amount absorbed by the plants. Arsenic bioavailability to plants is governed by soil physical and chemical characteristics, environmental conditions, kinetics of bioaccumulation and modifications to the rhizsosphere soil. In terrestrial environments As exists in four oxidation states (−III, 0, +III, and +V). Arsenate (As^{V}) and arsenite (As^{III}) predominate in aerobic soils and anaerobic environments (submerged soils), respectively (Mohan and Pittman, 2007). Abiotic factors such as changes in the redox potential and pH, and biotic factors (microorganisms) play a role in the interconversion of these two As forms (Zhao et al., 2010; Nearing et al., 2014). Dissimilatory reduction and detoxification are the two principal mechanisms for microbial arsenate reduction in the environment. For example, dissimilatory reduction occurs during anaerobic respiration, where As^{V} acts as a terminal electron acceptor and detoxification mechanism which transfers As^{V} into As^{III} and extrusion by an As^{III}-efflux pump. Abiotic As^{III} oxidation through Mn-oxides is faster than biotic oxidation (Parikh et al., 2010). Manganese oxides are widespread in the natural environment and readily serve as

Table 1
Selected references of arsenic (As) concentration in soil and groundwater in different parts of the world.

	Arsenic in soil			Arsenic in ground water		
Country/ Region	Location	As concentration (mg kg^{-1})	Reference	Location	As concentration (μg L^{-1})	Reference
Bangladesh	Tala Upazilla	3.2–51.8	Ahmed et al. (2011a, b)	Bengal Delta Plain	22–1000	Jiang et al. (2013)
India	Central India	16–417	Das et al. (2013)	Uttar Pradesh	43.75–620.75	Srivastava and Sharma (2013)
Pakistan	Punjab	7–35	Farooqi et al. (2009)	Punjab Mailsi	11–828	Rasool et al. (2016)
Taiwan	Taipei	4.71–513 dry weight	Lin et al. (2013)	Chianan Plain	10–1800	Chen and Liu (2007)
China	Inner Mongolia	154–238	Neidhardt et al. (2012)	Huhhot Basin Inner Mongolia	up to 1860	Guo et al. (2014); He et al. (2010)
USA	Hawaii	15–950	Hue (2010)	Tulare Lake	2600	Cutler et al. (2013)
Brazil	Minas Gerais	200–860	Bundschuh et al. (2012)	Minas Gerais	0.4–350	Mukherjee et al. (2006)
Chile	Chiu-Chiu	41.12–65.72	Díaz et al. (2011)	Northern Chile	60–80	Sancha and O'Ryan (2008)
Mexico	Durango	55–221.1	Morales et al. (2015)	Zimapan (Salamanca aquifer system)	190–650	Armienta and Segovia (2008)
Spain	Salamanca	70–5330	Otones et al. (2011)	Duero Cenozoic Basin	40.8 (mean)	Gómez et al. (2006)