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Arsenic contamination, speciation, toxicity and defense strategies in plants

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Abstract

This review explains the transport, mobility, resistance and detoxifcation of toxic metalloid arsenic (As) in plants. Arsenic is ubiquitously present in Earth's crust; however, numerous human interventions such as rapid industrialization use of As-based pesticides, insecticides and discharge of industrial wastes in water bodies leads to cumulative increase in As in the environment and has become a global challenge. Arsenic exists in diferent organic and inorganic forms, but inorganic forms such as pentavalent arsenate (As^V) and trivalent arsenite (As^{III}) are more toxic and actively taken up by plants. Its toxicity is marked by generation of reactive oxygen species (ROS) that are capable of degrading various biomolecules of the cellular systems. To keep the ROS under the limit, plants have an array of enzymatic antioxidants such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR) and glutathione-S-transferase (GST); and non-enzymatic antioxidant like ascorbate, proline, and cysteine. Contrary to this, As-hyper-accumulator plants survive under high concentration of As through the strenuous action of As^v reduction into As^{III} followed by the vacuolar compartmentalization of complex or inorganic As. Hence, this review focuses on the potential sources of As in the environment, its speciation and toxicity, and tolerance strategies in plants.

Keywords Antioxidants · Arsenate · Arsenic toxicity · Arsenite · Detoxifcation

1 Introduction

Arsenic (As) is a naturally occurring and ubiquitous toxic metalloid that persists in the environment often in combination with sulfur and other metals and afects the various life forms and thus become a global issue. The As contamination is widespread throughout the USA, China, Europe and Southeast Asia. However, its toxicity is very severe in countries of Southeast Asia such as Bangladesh, Vietnam and some states of India specially the West Bengal (Srivastava et al. [2016\)](#page-8-0). Weathering of Himalayan rocks containing sulfde minerals is the primary source of As deposition into rivers. Further, As bearing minerals when undergone

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 \boxtimes Sheo Mohan Prasad profsmprasad@gmail.com oxidation lead to the activation of iron (Fe) hydroxides, oxy-hydroxides, and oxides, thus contributing to As in soil. Besides this, the microbial leaching is another process that liberates the As in soil from Fe oxides (Fendrof et al. 2010). Further, several man-made actions including excessive use of As-based chemicals, insecticides, pesticides and fertilizers are responsible for the elevated level of As in the environment (Sharma et al. [2014\)](#page-8-1). Above-mentioned natural and anthropogenic activities raised the As content in ground and drinking water as it is in range of 10–50 μg L^{-1} which is toxic to various life forms (WHO [2001\)](#page-9-0). Organic forms such as monomethylarsonic acid (MMA), dimethylarsinic acid (DMA), tri-methyl arsine oxide (TMAO); inorganic forms such as arsenite (As^{III}) , arsenate (As^{V}) , arsenious acids and arsenic acids, are well known to induce toxicity in plants as well as in human beings (Tangahu et al. [2011\)](#page-9-1). Between inorganic forms, As^{III} predominates in reducing conditions while As^v in aerated soil condition (Mitra et al. [2017\)](#page-8-2). In context to plant system, As is absorbed in pentavalent form and is rapidly reduced to trivalent form either by arsenate reductase (ArsR) or by reduced glutathione (GSH). Substantially, As due to easy transportation and accumulation

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in plants targets various physiological and biochemical processes in plants. The As^{III} enters inside plant cell through nodulin-like intrinsic protein (NIPs) and aquaglyceroporins (Ma et al. [2008\)](#page-7-0) and thus reacts with the thiol (-SH) groups of macromolecule and disrupts the protein structure and damages the membrane structure leading to aberration in cellular processes (Zhao et al. [2010\)](#page-9-2). Further, uptake of As^V in plant is mediated by phosphate transporters (Pi transporters) and replaces the inorganic phosphate (iP) from the phosphorylation process and thereby interferes with the ATP synthesis (DiTusa et al. [2016](#page-7-1)). Mosa et al. [\(2012\)](#page-8-3) had observed that As-tolerance and transport is possible due to the involvement of a plasma membrane intrinsic protein (PIPs). On the other hand, it had also been demonstrated that tonoplast oriented efflux transporter (PvACR3) mediates As^{III} sequestration into vacuoles in the hyper-accumulator fern, *Pteris vittata* (Indriolo et al. [2010](#page-7-2)). Moreover, two ABC-type transporters from *Arabidopsis* have been shown as the major vacuolar As^{III} -phytochelatin complex transporters suggesting their role in As^{III} detoxification (Song et al. [2010\)](#page-8-4). On the other hand, the presence of Fe-plaques adjacent to the root enhances As-uptake in the roots of rice (Meharg and Rahman [2003](#page-8-5); Tiwari et al. [2014\)](#page-9-3) and signifes positive role of Fe in As transportation (Zhao et al. [2010](#page-9-2); Rahman et al. [2011](#page-8-6)).

The reports by Singh et al. ([2006,](#page-8-7) [2018](#page-8-8)) indicate that the As toxicity leads to cellular toxicity, membrane damage that increases the electrolyte leakage in plants disturbing membrane integrity; similar toxic effects were also reported in cyanobacteria in recent reports of (Patel et al. [2018](#page-8-9)). Moreover, the membrane damage is accompanied by an increase in malondialdehyde content, a product formed by peroxidation of membrane's lipid, pointing toward oxidative damage induced by As toxicity as reported in plants as well as in algal system (Singh et al. [2018](#page-8-8), [2020;](#page-8-10) Patel et al. [2018](#page-8-9), [2020](#page-8-11); Alsahli et al. [2020](#page-6-0)). To combat this stress condition, plants are endowed with antioxidant defense system including enzymatic antioxidants and also some metabolite like ascorbate (AsA), *γ*-Glu-Cys-Glytripeptide (GSH) and oligomer *γ*-Glu-Cys]n-Glyphytochelatin (PC) (Singh et al. [2015d](#page-8-12), [2020](#page-8-10); Ahmad et al. [2020a](#page-6-1)).

Besides this, several studies have demonstrated that As uptake, metabolism and translocation in plants are energydependent process (Ma et al. [2008;](#page-7-0) Zhao et al. [2010](#page-9-2)); the mechanisms for As-accumulation, movement and detoxifcation in plants are not well known and need in-depth investigation. Area which is much remains to be learned is identifying the cellular metabolic processes that damaged by As. On the basis of above discussion and novel growing ideas, this review deals with several aspects of As-toxicity focusing on accumulation, transport, cellular detoxifcation mechanisms of plants and identifying key areas where further research is needed.

2 Arsenic in the environment

Although natural sources such as weathering of rocks and volcanic emissions along with discharge from hot springs are the primary sources of As in environment, moreover anthropogenic activities such as mining, smelting, industries, use of arsenic-based pesticides, herbicides, wood preservatives, as well as food additives also contribute in (Bhattacharya et al. [2002](#page-7-3); Singh et al. [2015a,](#page-8-13) [b\)](#page-8-14). Being a naturally occurring toxic metalloid, the average concentration of As ranges from 1.5 to 5 mg kg^{-1} (as reviewed by Sharma et al. [2014\)](#page-8-1) and ranks 20th in abundance on the Earth's crust, 14th in the seawater, and 12th in the human body (Mandal and Suzuki [2002](#page-7-4)) though higher concentrations have been found in fne-grained argillaceous sediments and phosphorites. Besides this, As concentration in the reducing marine sediment is 3000 mg kg⁻¹ (Mandal and Suzuki [2002](#page-7-4)) and in seawater is > 2 μg L⁻¹ (Ng [2005\)](#page-8-15) As. In freshwater, the value ranges from 0.15 to 0.45 μg L^{-1} (Bissen and Frimmel [2003](#page-7-5)). One of the key factor that is responsible for As contamination is digging of tube wells deep inside the crust which leads to weathering of rocks and therefore release of As into the groundwater. However, As is found at low concentration in natural water but at some places the levels of arsenic in drinking water are above the maximum permissible concentration i.e. 50 μ g L⁻¹ while the recommended level is 10 μg L^{-1} as stated by Environmental Protection Agency; EPA (Sharma and Sohn [2009\)](#page-8-16). The As contents in environment have been summarized in Table [1](#page-1-0). The soil content of As difers in diferent geographic regions, e.g. it ranges from 0.1 to 40 mg kg⁻¹ (mean 6 mg kg⁻¹). The lowest concentration of As is found in sandy soils, whereas higher

Table 1 Concentration of As in environment

Material	Concentration	Reference
Earth's crust	3 mg kg^{-1}	Kabata-Pendias et al. (1984)
Uncontaminated soils	$< 10 \text{ mg kg}^{-1}$	Peterson et al. (1981)
Contaminated soil	0.1–97 mg kg^{-1}	Kamiya et al. (2009)
Seawater	$<$ 2 µg L ⁻¹	Kabata-Pendias et al. (1984)
Unpolluted surface water and ground- water	$1-10 \mu g L^{-1}$	Bissen and Frimmel (2003a, b)
Thermal waters	8.5 mg L^{-1}	Sharma and Sohn (2009)
Stream/river	5.0–4000 mg kg^{-1}	Mandal and Suzuki (2002)
Drinking water	$50 \mu g L^{-1}$	Sharma and Sohn (2009)
Lake	2.0–300 mg kg^{-1}	Mandal and Suzuki (2002)
Air	$0.4 - 30$ ng m ⁻³	Helsen (2005)

concentrations are found in alluvial and organic soils, thus afecting plant growth and productivity. Methylation of inorganic arsenic compounds is performed by microorganisms which under oxidizing environment convert inorganic forms into MMA, DMA and TMAO (Drewniak and Sklodowska [2013\)](#page-7-6). Various forms of arsenic have been shown in Table [2.](#page-2-0) Excessive concentration of As signifcantly contaminates the agricultural land and soil and thus reduces the plant growth and productivity by interfere with mineral uptake, physiological and biochemical processes.

3 Arsenic speciation and their uptake mechanism

Arsenic exists in both organic and inorganic species and generates toxicity responses in the environment. The available form of As for the plant uptake is As^{III} , As^v, MMA and DMA; this section deals with the uptake mechanism of these available form As in plants.

Arsenite; As^{III} uptake – Arsenite presented predominantly as a neutral molecule (arsenous acid) under the normal pH range and plants uptake As^{III} in form of $As(OH)₃$. As^{III} enters into the plant root through NIP aquaporin channels present on plasma membranes (Ma et al. [2008\)](#page-7-0). NIP is a subfamily of the major intrinsic proteins (MIPs) collectively known as water channels (Bienert et al. [2008\)](#page-7-7). Plant aquaporins mediateà the transport of water or small neutral solutes and are classifed into four subfamilies with respect to the localization and sequence homology includes tonoplast intrinsic proteins (TIPs), small basic intrinsic proteins (SIPs), PIPs, and NIPs (Maurel et al. [2008\)](#page-7-8). There are 35 and 39 NIPs reported in *Arabidopsis thaliana* and *Oryza sativa* (rice) genomes, respectively (Wallace and Roberts [2004](#page-9-4)). NIPs are further sub-classifed into three subgroups: NIP I, II and III based on the sequence similarity of the plants (Wallace and Roberts [2004\)](#page-9-4). Rice plants express

Table 2 Diferent forms of As compounds in environment

Name	Formula
Arsenobetaine	$(CH3)3As+CH2COO-$, AB
Arsenocholine	$(CH3)As+CH2CH2OH, AC$
Monomethylarsonic acid	$CH3AsO(OH)2$, MMA ^V
Dimethylarsinic acid	(CH_3) ₂ AsO(OH), DMA ^V
Monomethylarsenous acid	$CH3As(OH)2$, MMA ^{III}
Dimethylarsenous acid	(CH_3) , AsOH, DMA ^{III}
Trimethylarsinic oxide	$(CH3)3 AsO, TMAO$
Methylarsine	CH ₃ AsH ₂
Dimethylarsine	(CH_3) ₂ AsH
Trimerthylarsine	$(CH_3)_3As$

all three types of NIPs for As^{III} transport such as NIPI (OsNIP1;1), NIPII (OsNIP3;1), and NIPIII (OsNIP2;2- Lsi6 and OsNIP2;1-Lsi1) (Mitani et al. [2008\)](#page-8-17). Further, role of NIPs is bidirectional either mediated $As³⁺$ influx across membrane or mediated As^{III} efflux (detoxification), proved by cloning the isoforms of NIPs from *O. sativa* (OsNIP2;1 and OsNIP3;2), *Lotus japonicus* (LjNIP5;1 and LjNIP6;1), and *A. thaliana* (AtNIP5;1 and AtNIP6;1) (Bienert et al. [2008](#page-7-7)). Among them only the NIP III appears to be unique to transport activities for other solutes such as undissociated $As^{\overline{III}}$ (Ma et al. [2008;](#page-7-0) Zhao et al. [2010\)](#page-9-2). However, the mechanisms of specifcity of transporting substrates among diferent NIPs are unknown (Zhao et al. [2010](#page-9-2)). In yeast the majority of As^{III} uptake occurs through hexose permeases (Liu et al. [2004\)](#page-7-9). In *Pteris vittata* (As hyper-accumulating plant), As remains mobile and rapidly transported through the xylem to the fronds (Pickering et al. [2006;](#page-8-18) Su et al. [2008\)](#page-9-5) while As^{III} is taken up by glycerol-transporting channels in *O. sativa* (Mishra and Sinha [2012\)](#page-8-19).

Arsenate; As^v uptake – The As^v is more toxic under aerobic conditions than anaerobic (Wu et al. [2011](#page-9-6)). Interestingly, the chemical behavior of As^v is similar to phosphate Pi (V) and they are the chemical analogs of corresponding phosphate ions. Hence, As^v and Pi may be taken up by the same plasma membrane transport system via high-affinity Pi transporters (Zhao et al. [2009\)](#page-9-7). Shin et al. ([2004](#page-8-20)) and others researchers have conducted physiological studies and found competitive inhibition of As^v uptake by Pi and isolation of As^v -resistant mutants in *Arabidopsis thaliana* defective in Pi transporters (Zhao et al. [2009\)](#page-9-7). In fact, some of these mutants were identifed on the basis of arsenate toxicity screening (González et al. [2005\)](#page-7-10). Furthermore, As^V represses genes concerned with the Pi starvation response, signifying that As^v may mislead the Pi sensor and interfere with the Pi signaling mechanism (Catarecha et al. [2007](#page-7-11)). Expression of phosphate transporters in plants governed by up-regulation of gene *Pht1* and number is varied among diferent plant species such as *A. thaliana* (nine genes, *Pht1;1* and *Pht1;4*), *O. sativa* (13 genes), *Zea mays* (six genes), *Hordeum vulgare* (eight genes), and *Triticum aestivum* (two genes) (Rausch and Bucher [2002;](#page-8-21) Gonzalez et al. 2005; Hasan et al. [2016](#page-7-12)). Different phosphate transporters may vary in their affinity for As^v. For example, the As hyper-accumulator *Pteris vittata* appears to have higher affinity for As^v than non-hyper-accumulator plants (Wang et al. [2002\)](#page-9-8). Additionally, Pi-uptake is highly regulated in plants and this regulatory system may also control As^v uptake and translocation. Presently, the relative affinities of various Pi transporters for As^v and Pi are poorly characterized. This information can be achieved by the assays of As^v/Pi transport activities in heterologous expression systems, such as yeast or *Xenopus laevis* oocytes (Chiou and Lin [2011\)](#page-7-13). Therefore, such information is needed

for manipulation of plants for either decreased or enhanced As^v uptake.

4 Uptake of methylated forms (MMA, DMA, TMA)

Microbes and alga via biomethylation and volatilization convert the toxic form of arsenic into less toxic methylated forms such as MMA^V , DMA^V and TMA which are present in the environment. A special type of NIP class transporter is OsNIP2; 1 also called as Lsi1 [known transporter for silicic acid (Si)] involve in transportation of methylated As species only for monomethylarsonic acid (MMA) not for dimethylarsinic acid (DMA) (Li et al. [2009\)](#page-7-14). In rice roots methylated As species are taken up partly through the NIP aquaporin. However, the rate of transport of MMA/DMA is slower than rate of As^V/As^{III} transport (Abbas and Meharg [2008](#page-6-2)), but their transport within the plant is much faster (Carey et al. [2011](#page-7-15)). On the whole, the methylated As species are taken up by roots at slower rates than inorganic As, but they are more mobile during the xylem transport from roots to shoots (Li et al. [2009](#page-7-14)). Further, micro-organisms are also responsible for converting the As into arsenocholine, arsenobetaine, and arseno-sugars, as reported in some terrestrial plants (reviewed by Dembitsky and Levitsky [2004](#page-7-16)).

5 Arsenic enters the agricultural feld

The As contaminates the groundwater and other water sources that are used for irrigation and drinking purposes, and this directly contaminates the agricultural feld and facilitates the entry of arsenic species that possess a serious threat to plants, animals as well as for human being. Besides this the agricultural land was also afected through the erosion, chemical run-off and release of organic matter from industrial effluents along with the widespread use of pesticides such as arsenicals that have led to considerable rise in the As concentrations in soil (Adriano [2001](#page-6-3)). Thus, As is widely distributed in the agriculture originating either from the parent soil material or from the discharge of As onto land as a result of human activities. Consequently, people and livestock are being exposed to As by the consumption of Asloaded drinking water and food grown in As-contaminated soil. Therefore, As contamination of natural waters has been one of the important environmental concerns because of its harmful effects on organisms directly by ingestion and inhalation or indirectly through the food chain pathways. Some experimental data have already been published regarding plant response at high As level in rice (Rahman et al. [2007](#page-8-22)), arum (Imamul-Huq et al. [2005](#page-7-17)), cowpea (Imamul-Huq et al. [2009](#page-7-18)), water spinach and Japanese mustard spinach (Shaibur and Kawai [2009\)](#page-8-23), bush bean and tomato (Xu et al. [2007\)](#page-9-9). South Asia and South-East Asia are the major rice growing areas of the world (Meharg [2004\)](#page-7-19). In these regions, rice felds are many times irrigated with underground water highly contaminated with As.

6 Toxicity responses in plants against arsenic stress

Some heavy metals (viz. Zn, Fe, Cu and Mn) fall under essential category as they are needed for the plant growth and metabolism. However, other metal and metalloids like Pb, Cd, Cr, Al and As are biologically non-essential and toxic. Arsenic (As) has long been known as a phytotoxic agent that imbalances physiological and biochemical processes in plants. The toxicity of As depends upon As speciation; generally inorganic As species are more toxic than organic forms to living organisms including plants, humans and other animals (Ng [2005](#page-8-15); Sharma and Sohn [2009](#page-8-16)). Arsenic signifcantly reduces the seed germination, morphological changes like leaf number, root and shoot length and photosynthesis which ultimately reduces the yield and fruit production (Cozzolino et al. [2010;](#page-7-20) Srivastava et al. [2011](#page-8-24); Singh et al. [2018](#page-8-8), [2020\)](#page-8-10). Arsenic interferes with the plant metabolic processes and targets growth, causes oxidative stress often leads to cell death (Singh et al. [2015a,](#page-8-13) [b](#page-8-14)). Foliar mass (fruit dry weight) of bean plants showed reduction of 50% while 84% reduction in fruit production or yield is observed as compared to control when treated with As. Moreover, As reduced the vegetative and root growth in tomato plants (Miteva [2002](#page-8-25)). Arsenic has been reported to cause 'straight head' disease which is a physiological disorder of rice in Bangladesh, characterized by sterility of the forates/spikelets leading to reduced grain yield (Rahman et al. [2008](#page-8-26)). Shaibur and Kawai [\(2009](#page-8-23)) reported that the shoot and root dry mass of sorghum was repressed by higher As levels. Moreover, a decrease in plants biomass with increasing As concentration in irrigation water has also been reported by Pigna et al. [\(2008\)](#page-8-27). In other studies, ATP, chlorophylls and photosynthesis have been reported in As-stressed plants (Singh et al. [2020;](#page-8-10) Ahmad et al. [2020b](#page-6-4)). As damages the chloroplast membrane and dismantles the photosynthetic process and consequently causes signifcant decrease in pigment content, rate of $CO₂$ fixation as well as functional activity of photosystem II (PSII) (Stoeva and Bineva [2003](#page-8-28)). Other physiological parameters such as efficiency of PS II, rate of transpiration, gas exchange and photo-protective compounds as carotenoids were found to be decreased under As stress (Stoeva et al. [2005](#page-9-10); Milivojevic et al. [2006](#page-8-29)). However, the change in the fuorescence parameters is not signifcantly observed in the primary leaves of soybean indicating less effect of As^V on photosynthetic electron transport. Further, As^V uncouples photophosphorylation that leads to decrease in ATP synthesis associated with inhibition in the germination of Z*ea mays* (Kaya et al. 2020). In early growth of plants, As^V increases the formation of reactive oxygen species (ROS) that damaged the lipids of membrane and increase in malondialdehyde equivalent content noticed in *Pteris ensiformis* (Hartley-Whitaker et al. [2001;](#page-7-22) Stoeva et al. [2005;](#page-9-10) Singh et al. [2006](#page-8-7); Ahsan et al. [2008](#page-6-5)). Over-accumulation of ROS eventually disturbs the redox state and afects the energy homeostasis of plants (Srivastava et al. [2011\)](#page-8-24). These ROS formed in plant either by formation of singlet oxygen through the excitation of O_2 or by leakage of electron (Foyer and Noctor [2005](#page-7-23)). These ROS also damage the macromolecules such as DNA, RNA, nucleic acids and proteins (Srivastava et al. [2011](#page-8-24)). For better growth performance under As stress, there is an equilibrium between production and elimination of ROS which decides the fate of a plant. During the un-stressful conditions, the antioxidants defense system maintains the pace with ROS and free radicals generation. Consequently, the biotic and abiotic stresses aggravate the production of toxic ROS. Afterward, the antioxidative defense system also gets enhanced. Moreover, ROS causes potent damage to the nucleic acids, nucleotides, amino acids, and proteins and afects peroxidation of membrane lipids under acute stress conditions (Møller et al. [2007](#page-8-30)). Lipid peroxidation afects the cellular processes and enhances the lipid-derived radicals (Ahmad et al. [2020b](#page-6-4)). Srivastava et al. [\(2005\)](#page-8-31) and Singh et al. [\(2006\)](#page-8-7) reported the induction of lipid peroxidation by As^v in *Pteris vittata* (hyper-accumulator) showing the ROS production which is a common end point of aerobic life.

To cope up with heavy metal stress, plant initiates a number of pathways and thiol mediated complexation is one of them (Bleeker et al. [2006](#page-7-24); Mishra et al. [2008\)](#page-8-32). Being a phosphate analogue, As^v significantly suppresses the gene that is up regulated under phosphate starvation (Abercrombie et al. [2008\)](#page-6-6). To cope up with the damaging efects induced by As, plants either increase the formation of low molecular weight antioxidants such as GSH and AsA or up regulate the antioxidant enzymes such as SOD, CAT and APX or also synthesized the proline and phenolic that have antioxidant property. Glutathione (GSH) plays an important role in As detoxification by chelating As (Ahmad et al. [2020a,](#page-6-1) [b](#page-6-4); Singh et al. [2015c](#page-8-33)). The antioxidants enzymes SOD, APX and GPX have been thoroughly studied in plants like rice, wheat and maize. Highly reactive superoxide radical can be converted to less active but longer lasting H_2O_2 through the action of SOD. SOD activity varies quite widely with As treatment. The enzyme activity shows elevated response at low level of As exposure in As-hyper-accumulator *P. vittata,* As-sensitive *Holcuslanatus* and As-tolerant *Zea mays*, and the activity either remains the same or decreases at higher As levels (Hartley-Whitaker et al. [2001](#page-7-22); Cao et al. [2004](#page-7-25);

Sinha et al. [2010](#page-8-34)). Thus, numerous physiological and biochemical processes are exaggerated due to As toxicity which depends upon its concentration, speciation, bioavailability, uptake and translocation in plants. Overall, we here summarize that under As stress, excessive ROS generate and that is a need to be scavenged for the maintenance of normal growth. Plants stimulate enzymatic antioxidants such as SOD, CAT and APX and non-enzymatic antioxidants such as ascorbate, GSH and α -tocopherol to destroy ROS (Ahmad et al. [2020a](#page-6-1), [b;](#page-6-4) Kaya et al. [2020](#page-7-21)). The precise mechanism of the As-induced generation of ROS is not well understand and has been postulated that As-detoxifcation mechanism, including the reduction of As^V to As^{III} and the induction of phytochelatins (PC) synthesis (Meharg and Hartley-Whitaker [2002](#page-8-35)), plays an important role in ROS generation (Møller et al. [2007\)](#page-8-30). The overall mechanism of As-induced toxicity and plant defense system is postulated in Fig. [1](#page-5-0).

7 Survival strategies of plants against As toxicity

To overcome the negative efects induced by toxic metal/ metalloids such as As, plants utilized a number of mechanisms to combat the stress conditions. Firstly, plants are well known to synthesize metal binding proteins or metal chelators such as GSH, metallothioneins (MTs) or phytochelatins (PCs) that actively accumulate As inside the vacuoles and makes it less available for plants (Verbruggen et al. [2009](#page-9-11)). Further, detoxifcation reactions also participate in conversion of toxic forms of As into less toxic forms and their efflux from the cell via specific transporters proteins (Dixit et al. [2016;](#page-7-26) Singh et al. [2017](#page-8-36)). Along with these mechanisms, production of compatible solutes or osmolytes such as glycinebetaine (Garg and Singla [2011](#page-7-27)), proline (Mishra and Dubey [2006\)](#page-8-37), and mannitol (Matysik et al. [2002\)](#page-7-28) also participates in minimizing the As-induced toxicity.

Natural strategies: mechanisms of arsenic detoxifcation in plants – The synthesis of specifc low molecular weight chelators plays an essential role to detoxify non-essential trace metalloids through binding and facilitate their transport into the vacuoles. Gamma-glutamylcysteine synthetase (g-ECS) and glutathione synthetase (GS) enzymes synthesize the tripeptide glutathione (Glu-Cys-Gly) (Schulz et al. [2008](#page-8-38)). GSH has been found to bind with a number of metals and metalloids and is responsible for the cellular redox balance mechanism, which is generally the target of metalloid toxicity. The high level of metalloid binding capacity of GSH has been found to increase cellular defense against oxidative stress. On the other hand, GSH is the precursor of PC; Gasic and Korban ([2007\)](#page-7-29) have postulated that the increasing GSH and PC synthesis alone seems to be insufficient to achieve As

Fig. 1 Schematic representation of arsenic mobility into the cell and detoxifcation pathways in plants

tolerance or accumulation. PCs are synthesized from GSH and this reaction is catalyzed by PC synthase (PCS) and this PCS are responsible for the post-translational activation by metalloid As. Nonetheless, there are few reports on the PC synthesis, that they are important factors for the basic As tolerance (Clemens [2006](#page-7-30)), but not in the hyper-tolerant plants or hyper-accumulators (Ernst et al. [2008](#page-7-31)). In *Arabidopsis thaliana*, PC deficiency leads to As hypersensitivity in the roots of non-hyper-tolerant plants; the major part of As is chelated by PC. In this regard, Kumari et al. [\(2017\)](#page-7-32) observed that the expression of PCs increased by 2.4-fold and 1.6 fold in leaves and roots of *Artemisia* grown under As stress. Similarly, Verbruggen et al. [\(2009\)](#page-9-11) also reported that the increase in GSH and PC synthesis in *A. thaliana* improved the tolerance and accumulation of both As^{III} and As^{V} species. It has been elucidated that As is a strong inducer of PC synthesis. Whenever rice is exposed to As^V , a number of genes and enzymes are up regulated for the GSH synthesis, metabolism and transport (Ahsan et al. [2008](#page-6-5)); therefore, under As stress condition the plants have higher demand for GSH (Bleeker et al. [2006\)](#page-7-24). Arsenite enters in plants either directly by plant root or its concentration found to increased inside the cell when reduction of As^v into $Asⁱⁱⁱ$ (reacts with metabolites having –SH groups) (Schulz et al. [2008\)](#page-8-38). In As hyper-accumulator plants like *Pteris vittata*, there is gradient of AsV present toward the vacuole from the cytoplasm and the reason behind this gradient is due to involvement of energy-dependent transport of As^{III} in tonoplast of the vacuoles (Zhao et al. [2010](#page-9-2)).

Arsenic detoxifcation is an important regulatory mechanism to minimize the As toxicity and a number of studies are conducted to prove that plants have inherent ability to reduce As^V into As^{III} and then in less toxic methylated species via the action of an enzyme arsenate reductase (AR) (Xu et al. [2007\)](#page-9-9). This process also mediates As efflux from cell to soil and maintains As bio-geochemical cycles (Shi et al. [2016](#page-8-39)). Gene encoding for AR is identifed in diferent plants such as *P. vittata* (*PvACR2*), rice (*OsACR2; OsACR2*), *A. thaliana* (*ATQ1* and *HAC1*), and *H. lanatus* (*HlAsr*) by using sequence homology with *ACR2*; the arsenate reductase gene was found in *Saccharomyces cerevisiae*. Plants with mutant *ACR2* gene showed higher As accumulation in stems, leaves or fruits leads the more susceptibility toward As stress (Dhankher et al. [2006\)](#page-7-33). Further, overexpression of *OsACR2;1* and *OsACR2*;2 in the rice plants shows higher resistance for As (Duan et al. [2007\)](#page-7-34).

Synthetic strategies: perception regarding genetic engineer-

ing – Plants have ability to extract the pollutants from the soil and water during the uptake of nutrients by the roots. The roots are capable to change more toxic forms to less toxic forms and store in vacuole of the cell. The phytoremediation technology depends upon the extraction through roots, transports through vascular system of plants and sinks to concentrate arsenic above the ground. Up-regulation of enzymes involved in the synthesis of GSH or PC is the key factor in enhancing the process of phytoremediation (Li et al. [2005;](#page-7-35) Guo et al. [2008](#page-7-36)) or over expresses the gene *GSH1* and *AsPCS1* (Guo et al. [2008\)](#page-7-36) that subsequently increases the As tolerance of plants. Further, in hyper-accumulator plants there is expression gene *arsC* encoded enzyme arsenate reductase in leaves of *Arabidopsis* induced by light that enhances the reduction of arsenate (Dhankher et al. [2002](#page-7-37)). By using bio-technological approach insertion the gene *arsC* from *P. vittata* in other plants increased the As phytoextraction, or detoxifcation mechanism. In crops plants, there is excessive formation of As-PC complex that sequestrated in the vacuoles of plants. Plants implemented another strategy to detoxify As by converting more toxic forms of As into less toxic forms and the process is known as bio-methylation mediated by enzyme methyl transferases.

The As-hyper-accumulator/metallophytes and macrophytes are available, so there is a possibility to develop cost-efective, ecofriendly As phytoremediation techniques. Thus As-safe crops can be grown in the presence of As contamination. Less accumulation of As to the edible parts of the plants would improve crops. The molecular biology proposes an alternative route to introduce hyper-accumulation traits into other plant species. Interestingly, the high level of As concentration has to be sustained by the action of many gene products which will be responsible for the arsenic uptake, arsenate reduction, root-toshoot translocation, vacuolar sequestration and diferent other aspects of phosphorus and sulfur metabolism. Therefore, there is a need to develop an integrated approach (viz. development of transgenic) for arsenic tolerance and accumulation in plants.

8 Conclusion

Arsenic (As) contamination or arsenic poisoning is a serious concern due to which plant agonizes various physiological and biochemical process. Increased industrialization has resulted in the elevated concentration of As in the environment that enters the agricultural felds through irrigation by contaminated water and thereby targets growth and reduces the crop yield and thereby afecting all the life forms i.e. plants, animals and humans health. Oxidative stress which is a resultant of As poisoning causes membrane damages and disrupts the structure of macromolecules and results in cell death; to combat with this stress condition plants possess well-developed antioxidant system, comprising of enzymatic activity and non-enzymatic content that keep the ROS under limit. On other hand, As biotransformation in the environment takes place by the seed, fruits, vegetable or plant parts. Therefore there is need to develop arsenic tolerant plant that survives under As concentration and concentrates As through plant parts and decontaminates the environment making it suitable for the living organism.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no confict of interest.

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