Chapter 15
Arsenic Tolerance and Signaling Mechanisms in Plants

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Abstract Arsenic (As) contamination is now prevalent in large areas of a number of countries. Arsenic stress during vegetative and reproductive phases of plant growth affects the growth, flowering, and fruit/grain development due to a number of physiological, biochemical, and molecular effects. The metabolism of carbon, nitrogen, and sulfur is affected along with changes in photosynthetic and respiratory processes. The avoidance of As toxicity requires fine-tuning of several processes starting from uptake and transport of As to As detoxification and prevention of stress manifestation. Thus, the regulatory processes promoting concerted action of several pathways become an important determinant of As stress tolerance of a plant. These include various phytohormones (auxins, jasmonates, ethylene, abscisic acid, salicylic acid, etc.), transcription factors, microRNAs, reactive oxygen and reactive nitrogen species, and kinases. It is also important to note that an early perception of arsenic entry into plants and signaling of the information to distant parts (leaves) ensure that plants remain prepared to tackle the As stress. Although the research on signaling aspects of arsenic stress is yet in the primary stage, the information available is of potential application and future research. The present work describes current knowledge on perception and signaling of As stress in plants.

Keywords Arsenic · MicroRNAs · Nitric oxide · Phytohormones · Reactive oxygen species · Transcription factors

1 Introduction

Arsenic (As) is a highly toxic metalloid having an array of toxic manifestations and carcinogenicity on various organisms, including humans (Duker et al. 2005). Arsenic is present in nature due to its use in agricultural and industrial sectors as well as due to natural biogeochemical factors leading to a large amount of As being

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R. Roychowdhury et al. (eds.), *Sustainable Agriculture in the Era of Climate Change*, https://doi.org/10.1007/978-3-030-45669-6_15

released in the environment (Shukla et al. 2017). Arsenic is posing serious health concerns specifically in West Bengal in India and Bangladesh. Exposure to As for a long time leads to the development of some serious symptoms such as skin lesions and different types of cancers (Kumar et al. 2015). There are many forms of As present in nature. These can be categorized into inorganic [arsenite: As(III) and arsenate: As(V)] and organic [monomethylarsonic acid: MMA, dimethylarsinic acid: DMA]. It is known that mono-, di-, and tri-methylated forms of As are produced in the soil by microbial processes (Mestrot et al. 2011). The entry of toxic As species in plants also occurs via competitive uptake through transporters of essential metals by the mechanism of ionic mimicry (Verbruggen et al. 2009; Ye et al. 2010). The influx of As(III) occurs primarily via nodulin 26-like intrinsic proteins (NIPs) class of aquaglyceroporins (Verbruggen et al. 2009; Bienert et al. 2008; Roychowdhury et al. 2018, 2019), whereas that of As(V) is driven by phosphate transporters (Wu et al. 2011).

The plants suffer toxicity when the As accumulation passes a certain level called threshold level (Srivastava et al. 2007). Arsenic exposure to plants affects several physiological, biochemical, and morphological processes which include germination, growth, and biomass production (Finnegan and Chen 2012). Arsenic toxicity impacts photosynthesis by reducing chlorophyll content in the leaves and by altering photosynthetic efficiency, electron transport rate, transpiration, etc. (Srivastava et al. 2013a). Arsenic, although a non-redox-active metalloid, also induces the production of reactive oxygen species (ROS) by inter-conversion of one ionic form to another and by overconsumption of reduced glutathione (GSH) in the process (Mylona et al. 1998). The oxidative stress conditions in the presence of As cause lipid peroxidation of membranes, damage proteins and DNA, and induce toxicity (Srivastava et al. 2011). Arsenic exposure also causes genotoxic effects like mitotic index depression, increased chromosomal aberrations like a break, fragments, c-metaphase, and multipolar arrangements (Gupta et al. 2018). By translocation to the shoot, the plant growth can be severely inhibited by As by arresting cellular expansion and biomass accumulation as well as by compromising plant reproductive capacity resulting in loss of yield and fruit production (Garg and Singla 2011).

In the presence of As, it becomes important for the plants to prepare and be equipped with mechanisms to tolerate the stress so as to survive and propagate. Plants tolerate As stress by an array of metabolic processes such as binding of As to thiol (-SH) containing ligands, glutathione (GSH), and phytochelatins (PCs) followed by As–thiol sequestration in vacuoles (Srivastava et al. 2007; Song et al. 2014; Tang et al. 2019), reduction of As(V) to As(III) (Chao et al. 2014; Shi et al. 2016), decrease in uptake of As by altered expression of transporters (Srivastava et al. 2014), protection against oxidative stress via activation of antioxidant enzymes and molecules (Srivastava et al. 2007; Roychowdhury et al. 2018, 2019), anatomical and morphological changes allowing plants to bind As to cell walls and to maximize nutrient uptake and translocation (root phenotype), etc. There are a large number of metabolites such as cysteine, glutathione, proline, α-tocopherol, γ-aminobutyric acid (GABA), and carotenoids which have a role in As tolerance (Pathare et al. 2013; Singh et al. 2016). The physiological and biochemical experiments to omics approach like transcriptomics, metabolomics, and proteomics have been employed to unravel the response networks for As tolerance in plants (Yu et al. 2012; Dixit et al. 2015; Srivastava et al. 2015; Roychowdhury et al. 2018, 2019). It is clear that a complex interplay of various mechanisms and their concerted response is important for tackling As stress. This necessitates the involvement of a number of regulatory and signaling processes to operate for the early perception and signaling of As stress and for coordinating various physiological, biochemical, molecular, and metabolic responses (Pathare et al. 2013). This chapter presents the knowledge gained in the field of As stress perception and signaling in plants.

2 Perception and Signaling of Arsenic Stress

The perception and signaling involve sensing the entry of As in plants and transfer this information among various plant cells and tissues from receptor systems to effector ones. The timely perception of the stress allows plants to respond appropriately to the incoming stress. Apart from the perception of the stress, the signal must reach to all cells, tissues, and organs so as to prepare them for stress that might reach to them sooner or later. In the case of As stress, a few studies have been conducted that provide valuable insights into the perception and signaling of As stress. Some of the well-known signaling mechanisms constitute mitogen-activated protein kinases (MAPKs), reactive oxygen species (ROS) and reactive nitrogen species (RNS), hormones [abscisic acid (ABA), jasmonic acid (JA) and other jasmonates, salicylic acid (SA), ethylene, brassinosteroids, etc.], microRNAs, and transcription factors. In the following sections, the available knowledge is presented to showcase the aspects of perception and signaling of As stress in plants (Roychowdhury et al. 2018, 2019).

3 Phytohormones

Phytohormones regulate crucial physiological responses of plants during growth, such as cell division, cell differentiation, organ formation, leaf senescence, flowering, and grain development, and also in response to various abiotic and biotic stresses (Shukla et al. 2017). Auxins play the role of key regulators of phenotypic changes that directly affect responses of plants to the stresses (Nibau et al. 2008). The auxin accumulation takes place at the root tip, and the plant apical tissues are a place of auxin synthesis. Therefore, auxins are transported downward via phloem toward the tip of the root (Benkova et al. 2003). The exogenous supply of an auxin, indole-3-acetic acid (IAA), was found to improve the growth of *Brassica juncea* and enhance tolerance of plants under As stress. The effects were found to be mediated through changes in the expression of microRNAs like miR167, miR319, and miR854 (Srivastava et al. 2013b). Selenium (Se) is known to ameliorate As toxicity in rice plants (Chauhan et al. 2017). The exogenous supply of auxin along with Se further augments As tolerance of rice plants in comparison to that achieved through Se alone supply (Pandey and Gupta 2015). In *A. thaliana*, mutants of auxin transporters *aux1*, *pin1*, and *pin2* have been found to be more sensitive to As(III) as compared to WT plants. Further, the supply of auxin transport inhibitors also compromised plants' tolerance to As(III) of WT plants, while exogenous IAA supply improved As(III) tolerance of *aux1* mutants (Krishnamurthy and Rathinasabapathi 2013).

Jasmonates play a vital role in mediating several processes involved in the overall development of plants and abiotic and biotic stress response. Some of the developmental processes include senescence, tuber formation, pollen maturation, root growth, and interactions with other organisms (Carvalhais et al. 2015). The activation of jasmonic acid (JA) signaling pathway happens due to the conjugation of JA to the amino acids, i.e., L-isoleucine (Ile), which produces an active hormone called as (3R, 7S)-jasmonoyl-L-isoleucine (JA-Ile). The F-box protein Coronatine-Insensitive 1 (COI1) is a co-receptor of JA-Ile, which binds with JA-Ile, for ubiquitin-mediated degradation of JAZs (jasmonate ZIM-domain) proteins. This releases transcription factors, i.e., MYC2, which activate or repress gene expression associated with JA (Carvalhais et al. 2015). JAs can regulate sulfur metabolism and the level of GSH and PCs to ameliorate the toxic effects of metals (Maksymiec et al. 2007). Jasmonates are suggested to play the primary role in sensing the entry of As in plants via an indirect perception of As-induced stress to sulfur metabolism (Srivastava et al. 2009). The significant changes in the level of JA and methyl jasmonate (MeJA) were observed in As-stressed *B. juncea.* Further, the exogenous supply of JA was found to improve the growth of *B. juncea* plants as well as tolerance under As stress (Srivastava et al. 2013b). An involvement of JA in the responses to As stress in rice and *B. juncea* was also suggested when the transcriptome analysis showed significant upregulation of genes of JA biosynthesis and JAZs (Yu et al. 2012; Srivastava et al. 2015).

Abscisic acid (ABA) is a derivative of carotenoid and is an essential phytohormone, which plays a vital role against various kinds of stresses like low temperature, heat stress, drought, salinity, and metals (Vishwakarma et al. 2017). In transcriptomic analyses in rice and *B. juncea* under As(III) and/or As(V) stress, a change in ABA metabolism genes was noticed (Chakrabarty et al. 2009; Srivastava et al. 2015). It has been found that there is an increase in ABA synthesis under As stress in *B. juncea*. An evidence of interaction between ABA and miR159 was also found to have an impact on As stress response (Srivastava et al. 2013b). Salicylic acid (SA), a phenolic compound, is synthesized from phenylalanine in cytoplasm and chorismate in chloroplast by two different pathways (Vlot et al. 2009). The main functions of SA include seed germination, respiration, and thermal tolerance. It plays a vital role in plant response to a variety of abiotic stresses (Vlot et al. 2009). A reversion in the plant growth and oxidative stress upon the exogenous application of SA in the rice has been found under As stress. It could also reduce As translocation to shoots through changes in As transporter genes (Singh et al. 2015). SA also acts as a direct scavenger of ROS and affects oxidative metabolism and increases antioxidant potential (Singh et al. 2015). An interplay of SA and nitric oxide (NO) in the regulation of As stress is also demonstrated. In rice plants exposed to As(III), a decline in the level of NO and SA was noticed. Upon exogenous supply of SA, the level of SA, as well as NO, was found to increase through the increase in the activity of nitrate reductase. The supplementation of SA was found to reduce As concentrations while increasing that of nutrient elements like Zn, Mn, and Fe in rice shoots (Singh et al. 2017). Ethylene is the only plant hormone present in a gaseous state. This hormone is involved in processes like fruit ripening and abscission and root hair formation (Lewis et al. 2011). An increase in ethylene levels under metal stress has been found, and the role of ethylene in the regulation of metal stress responses of plants is demonstrated (Masood et al. 2012; Khan and Khan 2014). However, the role of ethylene in As stress responses of plants is not yet elucidated. Nonetheless, ethylene biosynthesis and ethylene-responsive genes have been observed to upregulated during transcriptome analysis of rice plants upon As exposure (Chakrabarty et al. 2009; Yu et al. 2012).

Cytokinins are derivatives of adenine and are involved in cell division, nutrient metabolism, nodulation, and circadian rhythms (Argueso et al. 2010). Cytokinins act as negative regulators of lateral root formation via interplay with auxins (Laplaze et al. 2007). Srivastava et al. (2009) found that in the presence of As stress, *B. juncea* shows downregulation of cytokinin response 1 (CRE1) gene, which is a cytokinin receptor. The negative effect on cytokinin reception led to an increase in the expression of sulfate transporters. Mohan et al. (2016) developed transgenic *Arabidopsis thaliana* lines having a constitutive expression of cytokinin oxidase/dehydrogenase 1 (CKX1) gene to achieve cytokinin depletion. It was found that cytokinin-depleted lines became As(V) tolerant through efficient suppression of As(V) transporter and PHT1;1 and also due to increase in the expression of As(V) reductase gene as well as due to increase in the level of thiol compounds (GSH and PCs). Gibberellins are a large family of plant growth hormones associated mainly with seed germination, leaf expansion, and floral development (Daviere and Achard 2013). The role of gibberellins in metal stresses like cadmium, nickel, and lead is revealed (Meng et al. 2009; Sharaf et al. 2009). However, the role of gibberellins in As stress responses of plants is suggested only due to observed changes in the expression of gibberellin synthesis and response genes (Chakrabarty et al. 2009). The above discussion implicates that coordinated action of several phytohormones operates under As stress to fine-tune plants' responses. However, more experiments are needed in the future to delineate the in-depth mechanisms.

4 Reactive Oxygen and Nitrogen Species (ROS and RNS)

The oxygen-dependent life on Earth also entails the continuous production and dismutation of reactive oxygen species (ROS) due to the transfer of electrons or excess energy to oxygen. The process normally occurs at an optimal rate, and the role of ROS as an essential component of growth and development is known (Mittler 2002).

The ROS include singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide radical ($O_2\cdot-$), and hydroxyl radical ($\cdot OH$) (Foyer and Noctor 2000). However, in the presence of metals including As, the rate of ROS production may surpass that of ROS dismutation leading to an excess of oxygen molecules wandering to react with biomolecules. The excessive ROS production under As stress causes oxidative stress and damages membranes, proteins, and DNA (Srivastava et al. 2011). However, ROS stimulation under As stress can also act as a signaling component. In fact, an increase in the activity of prooxidant enzymes like ascorbate oxidase and NADPH oxidase, involved in ROS generation, has been observed in response to As stress (Srivastava et al. 2011). Research on NADPH oxidase mutant lines of *A. thaliana* demonstrated the role of another prooxidant enzyme, glycolate oxidase, in As-induced stress responses (Gupta et al. 2013). Further, ROS are known to interact with other signaling components like NO and phytohormones (Shukla et al. 2017; Singh et al. 2017).

Reactive nitrogen species constitute NO and compounds derived from NO reaction with biomolecules like S-nitrosothiols (Shukla et al. 2017). NO plays a critical part in abiotic and biotic stress responses of plants due to its ability to interact with several biomolecules, proteins, ROS, and phytohormones (Mengel et al. 2013; Grun et al. 2016). NO interacts with biomolecules in three types of mechanisms: S-nitrosylation, metal nitrosylation, and tyrosine nitration (Lamotte et al. 2014). S-nitrosylation is the reaction of NO with thiol-containing molecules and proteins. Metal nitrosylation is the binding of NO to transition metals to form metalloproteins. In tyrosine nitration, a nitro group is added to tyrosine residues. Nitric oxide supplementation has been found to play a vital role in the reduction of As accumulation in rice (Singh et al. 2015). Involvement of NO and SA interaction in As stress responses of rice was also demonstrated (Singh et al. 2017). As induced, nitro-oxidative stress occurs due to the effect of As on the activity of glutathione reductase and *S*-nitrosoglutathione reductase. This, in turn, decreases GSH and GSNO content (Leterrier et al. 2012). NO-mediated protection against As toxicity has also been noticed in *Luffa acutangula* (Singh et al. 2013), *Hordeum vulgare* (Shukla et al. 2015), and *Pistia stratiotes* (Farnese et al. 2017). NO supplementation improved plant physiology and maintained the organellar structure. In rice plants, NO supplementation has been found to reduce As-induced oxidative stress and improve thiol metabolism and expression of genes (Praveen and Gupta 2018). In *B. juncea*, exogenous supply of sodium nitroprusside (NO donor) was found to reduce As accumulation and improve growth and mineral nutrient status of plants. The supply of NO was also found to affect nitrogen metabolism and the expression of auxin transporter genes (Praveen et al. 2019).

5 MicroRNAs (miRNAs)

Posttranscriptional regulation of mRNAs by other small RNAs is an important component of gene expression regulation (Axtell 2013; Bej and Basak 2014). MicroRNAs (miRNAs) are highly conserved small RNAs of 20–24 nucleotides that regulate the expression of genes by targeting specific mRNAs. The miRNAs either cleave the target mRNA or decrease translation of mRNA into protein (Xie et al. 2015; Stepien et al. 2017; Srivastava and Pathare 2017). These miRNAs regulate several processes of growth and development of plants, metabolic pathways, and enzymatic reactions. In the case of abiotic and biotic stresses, including metals, the role of miRNAs has been revealed and has emerged as a crucial component (Srivastava and Pathare 2017). A few As-responsive miRNAs like miR168, miR169, miR319, miR416, miR444, miR820, miR1430, miR1437, etc. were computationally identified by Tuli et al. (2010). In another study comparing high and low As-accumulating varieties of rice, miRNA profiling identified a number of As(III)- and As(V)-responsive miRNAs. These miRNAs either demonstrated a common response to both As species and/or in both varieties or showed variety and As(III)-/As(V)-specific response (Sharma et al. 2015). The miR164, miR171, miR395, miR529, miR820, and miR1432 showed downregulation in both As(III) and As(V) stress, whereas miR408, miR1861, miR2102, and miR2907 showed upregulation. miR396 and miR528 showed a variable response in As(III) and As(V) stress, while miR399 and miR1846 demonstrated rice variety-specific response (Sharma et al. 2015). In *B. juncea*, As(V) stress-induced changes in the miRNA profile were evaluated for variable time points of 1 h and 4 h. The study identified a total of 69 miRNAs of 18 miRNA families that showed changes in expression pattern in time- and organ-dependent manner (Srivastava et al. 2013b). The upregulated miRNAs, miR426, miR472, and miR390, at 1 h depicted downregulation at 4 h, while the reverse trend was true for miR395. The time-dependent (6 h, 24 h, 72 h) and organ-dependent (root, shoot) real-time RT PCR analysis of few miRNAs (miR156, miR159, miR162, miR167, miR838, and miR854) further confirmed that expression of miRNAs changes dynamically and differentially in various tissues in response to As(V) stress in *B. juncea* (Srivastava et al. 2013b). The response of miRNAs also varies from plant to plant as seen in *O. sativa* and *B. juncea* (Liu and Zhang 2012, Srivastava et al. 2013b) where, for example, miR164 and miR172 were upregulated in *B. juncea* but showed downregulation in *O. sativa*. Further, the varying concentration of As(III) from low to high also has an influence on the miRNA profile of rice plants (Yu et al. 2012). In elemental interactions of As and selenium (Se) also, the role of miRNAs has been demonstrated Pandey et al. (2015). It is evident that miRNAs constitute a dynamic component of regulatory processes involved in As stress responses of plants, and the profile of miRNAs is an As concentration, As species, plant species, plant organ, and time-dependent process. Through dynamic changes, miRNAs affect crucial processes of metal detoxification (sulfur metabolism), metal uptake and distribution (transporters), metal stress (antioxidant mechanisms), and metal stress response (transcription factors, hormones)

(Curaba et al. 2014; Srivastava and Pathare 2017). In sulfur metabolism, miR395 regulates sulfur transporter (SULTR2;1) and ATP sulfurylase (APS), while miR838 and miR854 affect SULTR2;1 and SULTR2;2 and serine acetyl transferase (SAT) (Liang et al. 2010, Srivastava et al. 2013b). The regulation of Cu/Zn superoxide dismutase, the important enzyme of antioxidant defense dismutating superoxide ion to hydrogen peroxide, is achieved via miR398 (Bouche 2010). The level and signaling of phytohormones are also regulated by miRNAs, for example, miR160 and miR167 for auxin and miR319, miR168, and miR169 for jasmonates (Schommer et al. 2008).

6 Transcription Factors (TFs) and Kinases

The transcription process of mRNA synthesis and hence the gene expression are regulated by a number of transcription factors (TFs) (Anumalla et al. 2016). The role of several TFs is tuned in response to stress so as to achieve desirable expression of the required set of genes. A number of transcriptome studies have revealed the involvement of several families of TFs in As stress responses in plants like rice and *B. juncea*. The important TFs include WRKY, Myb, NAM, ATAF, NF-YA, AP2/EREBP, GATA, heat shock TFs, basis helix–loop–helix, homeobox, C2H2 zinc fingers, DOF zinc finger, etc. (Chakrabarty et al. 2009, Yu et al. 2012, Srivastava et al. 2015, Rai et al. 2015). The role of WRKY TF, WRKY6, was experimentally demonstrated by Castrillo et al. (2013) who found that As(V) stress-induced suppression of As(V)/phosphate transporter, PHT1;1, was regulated by WRKY6 in *A. thaliana*. Recently, the role of another WRKY TF, WRKY28, was studied in rice. WRKY28 was found to be an As(V)-inducible TF, and it regulated As accumulation in rice seedlings through effects on jasmonates (Wang et al. 2018). Mitogen-activated protein kinases (MAPKs) are a group of proteins, which are evolutionarily conserved and play important roles in signal transduction. MAPKs function in a cascade. Generally, the signals are relayed through MAPK kinase kinases (MAPKKKs), MAPK kinases (MAPKKs), and MAPK. In most cases, a single MAPK module transmits more than one signal in plants (Rodriguez et al. 2010). In the case of As, the role of MAPK3, MAPK4, and MKK4 is demonstrated in rice (Rao et al. 2011).

7 Conclusion and Future Perspective

The research on arsenic has mostly focused on arsenic chemistry in field and management practices to regulate arsenic levels in rice plant. The research on arsenic–plant interactions demonstrates involvement of various hormones, microRNAs, and kinases in the process of arsenic stress perception, signaling, and tolerance. However, the present picture mostly shows isolated changes in various signaling processes. The future research needs to bring about exact mechanisms of integration of various signaling molecules, hormones, and proteins so as construct a holistic picture. There is a need to reveal how arsenic infiltration is perceived by the plants. Hypothetically, arsenic entry might be perceived through interaction with a sensor protein, and this needs to be elucidated in coming years. The regulatory mechanisms involved in transporters' expression in roots, shoot, flag leaves, and seeds need to be understood so as to enable development of low-grain arsenic-accumulating rice varieties. The interconversion of arsenic species from one form to another constitutes an important mechanism of regulation of arsenic stress, its concentration in tissues, and its transport within plant. The process itself needs to be delineated in more detail. In addition, the aim should be to elucidate regulatory processes involved in arsenic metabolism. In conclusion, the research needs to focus on enhancing our knowledge about mechanistic details of arsenic–plant interactions.

References

Anumalla M, Roychowdhury R, Geda CK, Bharathkumar S, Goutam KD, Mohandev TSS (2016) Mechanism of stress signal transduction and involvement of stress inducible transcription factors and genes in response to abiotic stresses in plant. Int J Recent Sci Res 7(8):12754–12771

Argueso CT, Raines T, Kieber JJ (2010) Cytokinin signalling and transcriptional networks. Curr Opin Plant Biol 13:533–539

Axtell MJ (2013) Classification and comparison of small RNAs from plants. Annu Rev Plant Biol 64:137–159

Bej S, Basak J (2014) MicroRNAs: the potential biomarkers in plant stress response. American J Plant Sci 5(5):748

Benkova E, Michiniewicz M, Sauer M, Teichmann T, Seifertova D, Jurgens G, Friml J (2003) Local efflux dependent auxin gradients as a common module for plant organ formation. Cell 115:591–602

Bienert GP, Thorsen M, Schussler MD, Nilsson HR, Wagner A, Tamas MJ, Jahn TP (2008) A subgroup of plant aquaporins facilitates the bi-directional diffusion of $As(OH)_3$ and $Sb(OH)_3$ across membranes. BMC Biol 6:26

Bouche N (2010) New insights into miR398 functions in Arabidopsis. Plant Signal Behav 5:684–686

Carvalhais LC, Dennis PG, Badri DV, Kidd BN, Vivanco JM, Schenk PM (2015) Linking jasmonic acid signaling, root exudates, and rhizosphere microbiomes. Plant Microbe Interact 28:1049–1058

Castrillo G, Sánchez-Bermejo E, de Lorenzo L, Crevillén P, Fraile-Escanciano A, Mohan TC (2013) WRKY6 transcription factor restricts arsenate uptake and transposon activation in *Arabidopsis*. Plant Cell 25:2944–2957

Chakrabarty D, Trivedi PK, Mishra P, Tiwari M, Shri M, Shukla D, Kumar S, Rai A, Pandey A, Nigam D, Tripathi RD, Tuli R (2009) Comparative transcriptome analysis of arsenate and arsenite stresses in rice seedlings. Chemosphere 74:688–702

Chao DY, Chen Y, Chen JG, Shi SL, Chen ZR, Wang CC, Danku JM, Zhao FJ, Salt DE (2014) Genome-wide association mapping identifies a new arsenate reductase enzyme critical for limiting arsenic accumulation in plants. PLoS Biol 12:e1002009

Chauhan R, Awasthi S, Tripathi P, Mishra S, Dwivedi S, Niranjan A, Mallick S, Tripathi P, Pande V, Tripathi RD (2017) Selenite modulates the level of phenolics and nutrient element to alleviate the toxicity of arsenite in rice (*Oryza sativa* L.). Ecotox Environ Safety 138:47–55

Curaba J, Singh MB, Bhalla PL (2014) miRNAs in the crosstalk between phytohormones signalling pathways. J Exp Bot 65:1425–1438

Daviere JM, Achard P (2013) Gibberellin signaling in plants. Development 140:1147–1151

Dixit G, Singh AP, Kumar A, Dwivedi S, Deeba F, Kumar S, Suman S, Adhikari B, Shukla Y, Trivedi PK, Pandey V, Tripathi RD (2015) Sulfur alleviates arsenic toxicity by reducing its accumulation and modulating proteome, amino acids and thiol metabolism in rice leaves. Sci Rep 5:16205

Duker AA, Carranza EJM, Hale M (2005) Arsenic geochemistry and health. Environ Int 31:631–641

Farnese FS, Oliveira JA, Paiva EAS, Menezes-Silva PE, da Silva AA, Campos FV, Ribeiro C (2017) The involvement of nitric oxide in integration of plant physiological and ultrastructural adjustments in response to arsenic. Front Plant Sci 8:516

Finnegan PM, Chen W (2012) Arsenic toxicity: the effect on plant metabolism. Front Plant Sci 3:182

Foyer CH, Noctor G (2000) Oxygen processing in photosynthesis: regulation and signalling. New Phytol 146:359–388

Garg N, Singla P (2011) Arsenic toxicity in crop plants: physiological effects and tolerance mechanisms. Environ Chem Lett 9:303–321

Grun S, Lindermayr C, Sell S, Durner J (2016) Nitric oxide and gene regulation in plants. J Exp Bot 57:507–516

Gupta DK, Inouhe M, Rodriguez-Serrano M, Romero-Puertas MC, Sandalio LM (2013) Oxidative stress and arsenic toxicity: role of NADPH oxidase. Chemosphere 90:1987–1996

Gupta G, Mishra K, Srivastava S, Kumar A (2018) Cytotoxic assessment of chromium and arsenic using chromosomal behavior of root meristem in *Allium cepa* L. Bull Environ Contam Toxicol 100:803–808

Khan MIR, Khan NA (2014) Ethylene reverses photosynthetic inhibition by nickel and zinc in mustard through changes in PS II activity, photosynthetic nitrogen use efficiency, and antioxidant metabolism. Protoplasma 251:1007–1019

Krishnamurthy A, Rathinasabapathi B (2013) Auxin and its transport play a role in plant tolerance to arsenite-induced oxidative stress in *Arabidopsis thaliana*. Plant Cell Environ 36:1838–1849

Kumar S, Dubey RS, Tripathi RD, Chakrabarty D, Trivedi PK (2015) Omics and biotechnology of arsenic stress and detoxification in plants: current updates and prospective. Environ Int 74:221–230

Lamotte O, Bertoldo JB, Besson-Bard A, Rosnoblet C, Aimé S, Hichami S, Terenzi H, Wendehenne D (2014) Protein S-nitrosylation: specificity and identification strategies in plants. Front Chem 2:114

Laplaze L, Benkova E, Casimiro I, Maes L, Vanneste S, Swarup R, Weijers D et al (2007) Cytokinins act directly on lateral root founder cells to initiate root initiation. Plant Cell 19:3889–3900

Leterrier M, Airaki M, Palma JM, Chaki M, Barroso JB, Corpas FJ (2012) Arsenic triggers the nitric oxide (NO) and S-nitrosoglutathione (GSNO) metabolism in Arabidopsis. Environ Pollut 166:136–143

Lewis DR, Negi S, Sukumar P, Muday GK (2011) Ethylene inhibits lateral root development, increases IAA transport and expression of PIN3 and PIN7 auxin efflux carriers. Development 138:3485–3495

Liang G, Yang F, Yu D (2010) MicroRNA395 mediates regulation of sulfate accumulation and allocation in *Arabidopsis thaliana*. Plant J 62:1046–1057

Liu Q, Zhang H (2012) Molecular identification and analysis of arsenite stress-responsive miRNAs in rice. J Agric Food Chem 60:6524–6536

Maksymiec W, Wójcik M, Krupa Z (2007) Variation in oxidative stress and photochemical activity in *Arabidopsis thaliana* leaves subjected to cadmium and excess copper in the presence or absence of jasmonate and ascorbate. Chemosphere 66:421–427

Masood A, Iqbal N, Khan NA (2012) Role of ethylene in alleviation of cadmium-induced photosynthetic capacity inhibition by Sulphur in mustard. Plant Cell Environ 35:524–533

Meng H, Hua S, Shamsi IH, Jilani G, Li Y, Jiang L (2009) Cadmium-induced stress on the seed germination and seedling growth of *Brassica napus* and its alleviation through exogenous plant growth regulators. Plant Growth Regul 58:47–59

Mengel A, Chaki M, Shekariesfahlan A, Lidermayr C (2013) Effect of nitric oxide on gene transcription – S-nitrosylation of nuclear proteins. Front Plant Sci 4:293

Mestrot A, Feldmann J, Krupp EM, Hossain MS, Roman-Ross G, Meharg AA (2011) Field fluxes and speciation of arsines emanating from soils. Enviorn Sci Technol 45:1798–1804

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mohan TC, Castrillo G, Navarro C, Zarco-Fernandez S, Ramireddy E, Mateo C et al (2016) Cytokinin determines thiol-mediated arsenic tolerance and accumulation. Plant Physiol 171:1418–1426

Mylona PV, Polidoros AN, Scandalios JG (1998) Modulation of antioxidant responses by arsenic in maize. Free Radic Biol Med 25:576–585

Nibau C, Gibbs DJ, Coates JC (2008) Branching out in new directions: the control of root architecture by lateral root formation. New Phytol 179:595–614

Pandey C, Gupta M (2015) Selenium and auxin mitigates as stress in rice by combining the role of stress indicators, modulators and genotoxicity assay. J Hazard Mater 287:384–391

Pandey C, Raghuram B, Sinha AK, Gupta M (2015) miRNA plays a role in the antagonistic effect of selenium on arsenic stress in rice seedlings. Metallomics 7:857–866

Pathare V, Srivastava S, Suprasanna P (2013) Evaluation of effects of arsenic on carbon, nitrogen, and sulfur metabolism in two contrasting varieties of *Brassica juncea*. Acta Physiol Plant 35:3377–3389

Praveen A, Gupta M (2018) Nitric oxide confronts arsenic stimulated oxidative stress and root architecture through distinct gene expression of auxin transporters, nutrient related genes and modulates biochemical responses in *Oryza sativa* L. Environ Pollut 240:950–962

Praveen A, Pandey A, Gupta M (2019) Nitric oxide alters nitrogen metabolism and PIN gene expressions by playing protective role in arsenic challenged *Brassica juncea* L. Ecotox Environ Safety 176:95–107

Rai A, Bhardwaj A, Misra P, Bag SK, Adhikari B, Tripathi RD, Trivedi PK, Chakrabarty D (2015) Comparative transcriptional profiling of contrasting rice genotypes shows expression differences during arsenic stress. Plant Genome 8:1–14

Rao KP, Vani G, Kumar K, Wankhede DP, Misra M, Gupta M, Sinha AK (2011) Arsenic stress activates MAP kinase in rice roots and leaves. Arch Biochem Biophys 506:73–82

Rodriguez MC, Petersen M, Mundy J (2010) Mitogen-activated protein kinase signaling in plants. Annu Rev Plant Biol 61:621–649

Roychowdhury R, Khan MH, Choudhury S (2018) Arsenic in rice: an overview on stress implications, tolerance and mitigation strategies. In: Hasanuzzaman M, Nahar K, Fujita M (eds) Plants under metal and metalloid stress. Springer, Singapore, pp 401–415

Roychowdhury R, Khan MH, Choudhury S (2019) Physiological and molecular responses for metalloid stress in rice – a comprehensive overview. In: Hasanuzzaman M, Fujita M, Nahar K, Biswas J (eds) Advances in rice research for abiotic stress tolerance. Woodhead Publishing/Elsevier, USA, pp 341–369

Schommer C, Palatnik JF, Aggarwal P, Chetelat A, Cubas P, Farmer EE, Nath U, Weigel D (2008) Control of jasmonate biosynthesis and senescence by miR319 targets. PLoS Biol 6:e230

Sharaf AEMM, Farghal II, Sofy MR (2009) Role of gibberellic acid in abolishing the detrimental effects of Cd and Pb on the broad bean and lupin plants. Res J Agric Biol Sci 5:668–673

Sharma N, Tripathi A, Sanan-Mishra N (2015) Profiling the expression domains of a rice-specific miroRNAunder stress. Front Plant Sci 6:333

Shi S, Wang T, Chen Z, Tang Z, Wu Z, Salt DE, Chao DY, Zhao FJ (2016) OsHAC1;1 and OsHAC1;2 function as arsenate reductases and regulate arsenic accumulation. Plant Physiol 172:1708–1719

Shukla P, Singh S, Dubey P, Singh A, Singh AK (2015) Nitric oxide mediated amelioration of arsenic toxicity which alters the alternative oxidase (Aox1) gene expression in *Hordeum vulgare* L. Ecotox Environ Safety 120:59–65

Shukla A, Srivastava S, Suprasanna P (2017) Genomics of metal stress-mediated signaling and plant adaptive responses in reference to phytohormones. Curr Genomics 18:512–522

Singh VP, Srivastava PK, Prasad SM (2013) Nitric oxide alleviates arsenic-induced toxic effects in ridged *Luffa* seedlings. Plant Physiol Biochem 71:155–163

Singh AP, Dixit G, Kumar A, Mishra S, Singh PK, Dwivedi S (2015) Nitric oxide alleviated arsenic toxicity by modulation of antioxidants and thiol metabolism in rice (*Oryza sativa* L.). Front Plant Sci 6:1272

Singh S, Parihar P, Singh R, Singh VP, Prasad SM (2016) Heavy metal tolerance in plants: role of transcriptomics, proteomics, metabolomics, and ionomics. Front Plant Sci 6:1143

Singh AP, Dixit G, Kumar A, Mishra S, Kumar N, Dixit S (2017) A protective role for nitric oxide and salicylic acid for arsenite phytotoxicity in rice (*Oryza sativa* L.). Plant Physiol Biochem 115:163–173

Song WY, Yamaki T, Yamaji N, Ko D, Jung KH, Fujii-Kashino M, An G, Martinoia E, Lee Y, Ma F (2014) A rice ABC transporter, OsABCC1, reduces arsenic accumulation in the grain. Proc Natl Acad Sci U S A 111:15699–15704

Srivastava S, Pathare V (2017) Role of microRNAs in arsenic stress tolerance of plants. Intl J Plant Environ 3:9–15

Srivastava S, Mishra S, Tripathi RD, Dwivedi S, Trivedi PK, Tandon PK (2007) Phytochelatins and antioxidant systems respond differentially during arsenite and arsenate stress in *Hydrilla verticillata* (L.f.) Royle. Environ Sci Technol 41:2930–2936

Srivastava S, Srivastava AK, Suprasanna P, D'Souza SF (2009) Comparative biochemical and transcriptional profiling of two contrasting varieties of *Brassica juncea* L. in response to arsenic exposure reveals mechanisms of stress perception and tolerance. J Exp Bot 60:3419–3431

Srivastava S, Suprasanna P, D'Souza SF (2011) Redox state and energetic equilibrium determine the magnitude of stress in *Hydrilla verticillata* upon exposure to arsenate. Protoplasma 248:805–815

Srivastava S, Srivastava AK, Singh B, Suprasanna P, D'Souza SF (2013a) The effect of arsenic on pigment composition and photosynthesis in *Hydrilla verticillata* (L.f.) Royle. Biol Plant 57:385–389

Srivastava S, Srivastava AK, Suprasanna P, D'souza SF (2013b) Identification and profiling of arsenic stress-induced microRNAs in *Brassica juncea*. J Exp Bot 64:303–315

Srivastava AK, Srivastava S, Mishra S, D'Souza SF, Suprasanna P (2014) Identification of redox-regulated components of arsenate (AsV) tolerance through thiourea supplementation in rice. Metallomics 9:1718–1730

Srivastava S, Srivastava AK, Sablok G, Deshpande T, Suprasanna P (2015) Transcriptomics profiling of Indian mustard (*Brassica juncea*) under arsenate stress identifies key candidate genes and regulatory pathways. Front Plant Sci 6:646

Stepien A, Knop K, Dolata J, Taube M, Bajczyk M, Barciszewska-Pacak M, Pacak A, Jarmolowski A, Szweykowska-Kulinska Z (2017) Posttranscriptional coordination of splicing and miRNA biogenesis in plants. WIREs RNA 8:e1403

Tang Z, Chen Y, Miller AJ, Zhao FJ (2019) The C-type ATP-binding cassette transporter OsABCC7 is involved in the root-to-shoot translocation of arsenic in rice. Plant Cell Physiol (in press) 60:1525. https://doi.org/10.1093/pcp/pcz054

Tuli R, Chakrabarty D, Trivedi PK, Tripathi RD (2010) Recent advances in arsenic accumulation and metabolism in rice. Mol Breed 26:307–323

Verbruggen N, Hermans C, Schat H (2009) Mechanisms to cope with arsenic and cadmium excess in plants. Curr Opin Plant Biol 12:364–372

Vishwakarma K, Upadhyay N, Kumar N, Yadav G, Singh J, Mishra RK et al (2017) Abscisic acid signaling and abiotic stress tolerance in plants: a review on current knowledge and future prospects. Front Plant Sci 8:161

Vlot AC, Dempsey DMA, Klessig DF (2009) Salicylic acid, a multifaceted hormone to combat disease. Annu Rev Phytopathol 47:177–206

Wang P, Xu X, Tang Z, Zhang W, Huang X-Y, Zhao F-J (2018) OsWRKY28 regualtes phosphate and arsenate accumulation, root system architecture and fertility in rice. Front Plant Sci 9:1330

Wu Z, Ren H, McGrath SP, Wu P, Zhao FJ (2011) Investigating the contribution of the phosphate transport pathway to arsenic accumulation in rice. Plant Physiol 157:1498–1508

Xie M, Zhang S, Yu B (2015) microRNA biogenesis, degradation and activity in plants. Cell Mol Life Sci 72:87–99

Ye WL, Wood BA, Stoud JL, Andralojc PJ, Raab A, McGrath SP, Feldmann J, Zhao FJ (2010) Arsenic speciation in phloem and xylem exudates of castor bean. Plant Physiol 154:1505–1513

Yu LJ, Luo YF, Liao B, Xie LJ, Chen L, Xiao S, Li JT, Hu SN, Shu WS (2012) Comparative transcriptome analysis of transporters, phytohormone and lipid metabolism pathways in response to arsenic stress in rice (*Oryza sativa*). New Phytol 195:97–112