REVIEW ARTICLE

Nanoparticles mitigate arsenic stress in plants by modulating defence mechanisms

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Arsenic (As) stress greatly affects plant growth and production, threatening food security and also human health through the food chain. As alters various physiological processes that subsequently affect the normal metabolism in plants. The plants have evolved different mechanisms against stress, where nanoparticles (NPs) improve plant metabolism and the defence system, thereby alleviating As stress in it. This article discusses the effects of As in plants at different levels, and the role of NPs in modulating the plant defence system against As stress. This article may help encourage future research on plant protective mechanisms against stress and the significance of NPs in plant science and agriculture.

Keywords: Agriculture, arsenic stress, food security, nanoparticles, plant protective mechanisms.

THE toxic and carcinogen arsenic (As) is omnipresent, released into the environment by natural processes, as well as by anthropogenic activities[1]. The residues remain in the soil and get dissolved in groundwater, contaminating soil and water. Irrigation with contaminated groundwater also becomes an important route of As exposure, threatening plant growth and production.

As is taken up by plants as inorganic arsenite As(III) and arsenate As(V) and organic monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA). Different transporters are involved in the uptake and transportation of different species of As from soil to root and root to the above-ground parts of the plant body. As(V), the predominant form of As under oxidizing conditions, is transported by phosphate transporters due to structural similarity with inorganic phosphate (Pi). As(III) the dominant form in anaerobic environments, is an analogue of silicon and the analogy makes plants uptake the non-essential toxic As through aquaglyceroporin channels by competing with the element. Being a non-essential element, As induces toxicity in plants even at low concentrations. As(III) reacts with sulphhydryl groups of many proteins and enzymes, altering their conformation and activity, while As(V) replaces physiological processes Pi in various affecting the normal metabolism. As also induces the formation of reactive oxygen species (ROS), affecting ROS homeostasis and eventually oxidative damage to DNA, RNA, proteins and lipids[2]. Moreover, As gets accumulated in plant tissues; for example, 2.24 mg/kg As can be accumulated in rice grains. However, the maximum contaminant level (MCL) of As in rice grains is 200 μg/kg for white rice and 400 μg/kg for brown rice[3,4]. Hence As toxicity not only affects plants, but also human health through the food chain.

Arsenic stress in plants and its mitigation are a major concern globally. Increased ROS production by As exposure is counteracted by the stimulation of antioxidant enzymes as reported in many studies, revealing a strong association of antioxidant enzymes and metabolites with As tolerance in plants[5,6]. Moreover, supplementation of essential elements is also an important strategy for mitigating As stress in plants, as this reduces As bioavailability and uptake in plants[7,8]. Li *et al.*[9] in ryegrass under As stress revealed the major association of nutrient absorption and antioxidant enzymes with As stress tolerance. Minimization of As uptake and detoxification of As-induced ROS are important strategies for As stress mitigation in plants.

Nanoparticles (NPs), due to their distinctive properties such as high surface energy and high catalytic efficiency with strong adsorption ability, are a prominent tool against abiotic stress in plants[2]. NPs increase nutrient uptake and ROS scavenging enzymes in plants. It has been reported that the application of essential elements in the form of NPs effectively increases their absorption and activity of antioxidants, while reducing the uptake and toxicity of As in plants[10]. Bidi *et al.*[11] demonstrated that Fe NPs alleviated As stress in rice by improving Fe uptake and strengthening the antioxidant defence system, revealing the significant role of NPs in alleviating As phytotoxicity in plants. The utilization of NPs was found to be promising against As stress in plants. Therefore, this article deals with the plant morphological, physiological, biochemical and genetics due to As exposure and the promising role of NPs in the mitigation of As stress in plants, which is quite essential for food security.

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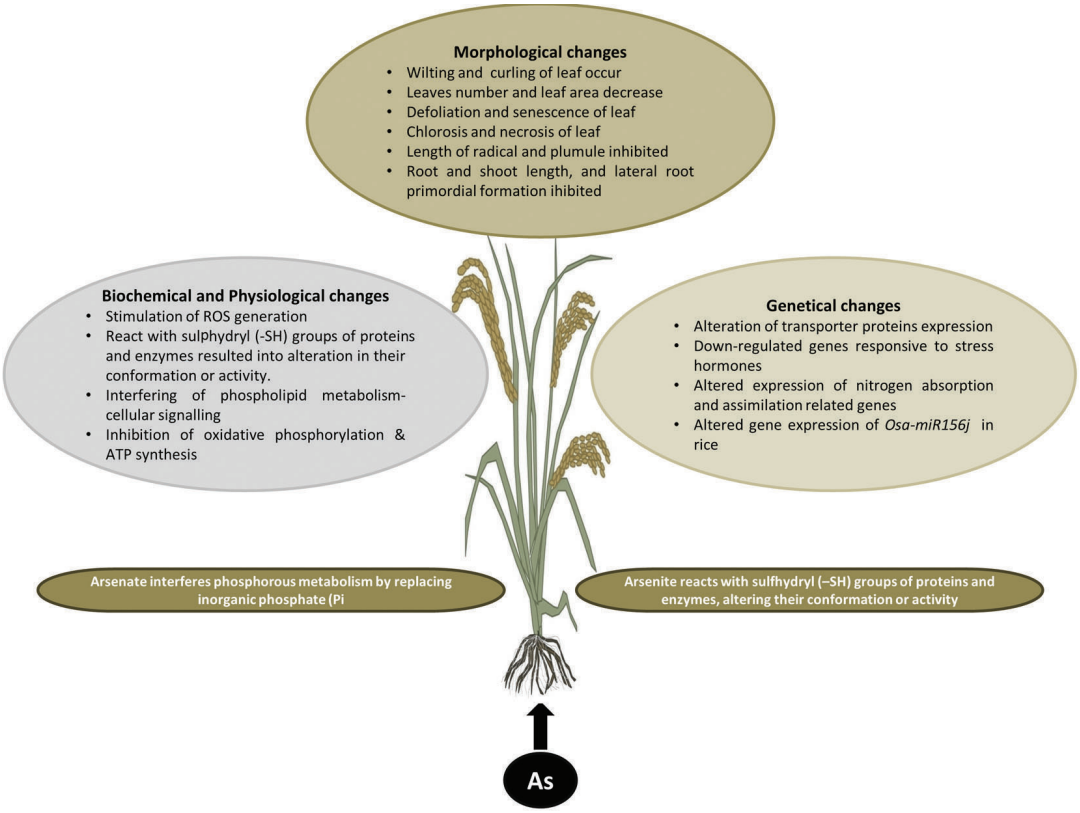

Figure 1. Effects of arsenic (As) at different levels in plants.

Arsenic metabolism and toxicity in plants

Since As is a non-essential and toxic metalloid, it has no essential function in plant metabolism. It alters the normal metabolism of plants by entering the tissues through various transporters of essential elements. Plants have evolved different mechanisms against toxicity induced by As, the important ones being the activation of antioxidant enzymes and non-enzymic antioxidants that can scavenge ROS; complexation with ligands and vacuolar sequestration. However, As stress induces morphological, physiological, biochemical and molecular changes in plants (Figure 1).

Morphological changes

Arsenic exposure leads to morphological changes in different plants. Niazi *et al.*[12] observed a significant reduction in plant height, leaf area and the number of leaves in *Brassica napus* and *Brassica juncea* under As treatment. Singh *et al.*[13] reported 63% and 82% reduction in root length of mung bean seedlings under 10 and 50 µM As respectively, which is consistent with the finding of Nath *et al.*[14], where rice root length was reduced by two-fold under 100 µM As with respect to control. Thounaojam *et al.*[15] demonstrated the detrimental effects of As on germination and length of radical and plumule of rice seedlings, which could be due to the toxic effect of As on seed metabolic activities. As causes wilting, curling and senescence of leaves, leaf chlorosis and necrosis, and a reduction in the number of leaeves[16]. Morphological changes induced by As on the root system architecture of rice have been reported by Ronzan *et al.*[17], where 100 µM As significantly reduced adventitious root length and lateral root primordial formation with respect to control. This was due to the interruption of indole acetic acid (IAA) biosynthesis and transport. Atabaki *et al.*[18] also provided insights on the impact of different concentrations of As on the morphological characteristics of water mimosas. It has been reported that As reduces the number and growth ratio of leaves and roots, and also root and shoot diameter with the increase in concentration and duration of treatments. Moreover, As treatments caused changes in the colour of leaves and roots. The leaves turned yellow from green and roots turned brown to pinkish over time, leading to wilting and consequently death of the plants.

Biochemical and physiological changes

As induces ROS generation mainly through the mitochondrial electron transport chain[19]. It inhibits the activity of succinic dehydrogenase enzyme resulting in the uncoupling of oxidative phosphorylation with a significant generation of ROS. Moreover, during the reduction of As(V) to

As(III) and synthesis of phytochelatin (PC), reactive oxygen species (ROS) is formed leading to oxidative damage to plant biomolecules[20]. Excessive ROS causes lipid peroxidation, protein carbonylation and DNA base oxidation. Besides, the literature reveals that the generated ROS can alter cell signal transduction, including Nrf2-antioxidant response element (ARE) signalling pathway, microRNAs (miRNAs), mitophagy pathway, tyrosine phosphorylation system, mitogen-activated protein kinases (MAPKs), nuclear factor κB (NF-κB), and activator protein-1 (AP-1). As(III) inhibits the activity of photosynthetic enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) by binding with the vicinal dithiol (Cys172-Cys192) of the enzyme, affecting the fixation of carbon dioxide (CO_2) in plants[21]. As(III) also binds with the co-factor of enzyme complexes and inhibits them. For example, Bergquist *et al.*[22] showed that As(III) binds with lipoic acid, the co-factor of pyruvate dehydrogenase complexes and α-oxoglutarate dehydrogenase complex (OGDC), affecting the cellular respiration. Gusman *et al.*[23] reported that photosynthetic rate declined by As treatment in lettuce plants with the inhibition of the CO_2 fixation process, which could be due to a decrease in the number and activity of RUBISCO. As can affect both photochemical and biochemical phases of photosynthesis by interfering with the activity of enzymes involved in the two phases. Decline in photosynthetic rate by As in plants has also been reviewed by Abbas *et al.*[1]. Impact of As on photosynthesis has been explained, where photosystems I and II, synthesis of chlorophyll, chloroplast membrane and CO_2 fixation are affected, leading to a decline in photosynthetic rate and yield. As also affects nitrogen metabolism in plants by altering activities of enzymes such as nitrate reductase, nitrite reductase and glutamate dehydrogenase, thereby reducing NO_3^- and NO_2^- contents and glutamic acid and glutamine ratio[24,25]. As(V) uncouples oxidative phosphorylation, resulting in the inhibition of ATP synthesis[26]. ATP is formed by phosphorylation of ADP in the mitochondria, but due to the interference of As(V) with the mitochondrial enzyme F_1F_0 ATP synthase, ADP–As(V) is formed, thereby inhibiting the normal metabolism. As(V) interferes with the activity of polynucleotide phosphorylase (PNPase), the enzyme that catalyses phosphorolysis and also the exchange of the terminal phosphate group of ADP and Pi. In the presence of AsV, PNPase catalyses the arsenolysis of RNA and ADP, resulting in AMP-arsenate[27]. As(V) also alters the activity of glycolytic enzymes by substituting the Pi group. Glyceraldehyde-3-phosphate dehydrogenase (GAPDH) is the glycolytic enzyme that catalyses the oxidative phosphorylation of D-glyceraldehyde 3-phosphate (G3P) to 1,3-biphospho-D-glycerate (1,3-BPG); but the presence of As(V) inhibits the formation of 1,3-BPG, landing to the formation of 1-arseno-3-phosphoglycerate (1-As-3-PG)[28]. Tariang *et al.*[29] also found that As altered the activity of hexokinase, phosphofructokinase and pyruvate kinase enzymes, which might have led to inhibition of carbohydrate metabolism.

Genetic changes

Pandey *et al.*[30] reported that As stress alters the gene expression of *Osa-miR156j* in rice, which is highly influenced by the duration of As exposure and different tissues of plant. It has been observed that the expression of *Osa-miR156j* was downregulated in different plant tissues at different developmental stages, where downregulation was more pronounced in root tissues at the developmental stage of the seedlings. Marotti *et al.*[31] also reported a huge decline in gene expression by ultrahigh diluted As_2O_3 in wheat plants with respect to the control plant. As_2O_3 application downregulated 71% of probe sets involved in the growth of the seedlings, revealing the under-expression of a majority of the affected genes by As_2O_3. However, genes responsive to stress hormones, including auxins and brassinosteroids and jasmonate and phenylalanine ammonia lyase, were activated with the application of As_2O_3, providing evidence for the strong gene-altering effect of As in wheat seedlings. Pan *et al.*[32] studied the dynamics of gene expression of As(III)-related transporters, viz. *OsLsi1*, *OsLsi2* and *OsABCC1* genes in rice plants. The relative expression of the *OsABCC1* gene was found to be linearly positively related to *OsLsi1* and *OsLsi2*, maximum at nine weeks of treatment. The relatively high expression of *OsLsi2*, *OsLsi1* and *OsABCC1* genes in roots and *OsLsi3*/*OsLsi6* and *OsABCC1* expression in the nodes/leaves and husks, and suppression of *OsABCC1* expression in the roots in 18–20 weeks led to high accumulation of As in the root and shoot. As altered the expression of transporters (Lsi1 and Lsi2) in rice, as demonstrated by Chen *et al.*[33], where As treatment induced a downregulation of the expression of Lsi1 and Lsi2 transporters in rice with respect to control. The differential expression of phosphate transporters (PHTs) in different genotypes of barley by As stress was reported by Zvobgo *et al.*[34]. Upregulation of PHTs in As-sensitive genotypes and downregulation in tolerant genotypes to a greater extent was observed, suggesting suppression of the expression of PHTs as the major mechanism for tolerance to As. It has also been reported that As stress induces transposon burst with the repression of As(V)/Pi transporter PHT1;1, thereby restricting As uptake in *Arabidopsi*[35]. WRKY transcription factor (WRKY6) was found to be responsible for repression in response to As stress, highlighting that WRKY6 is an essential component of As(V) repression of As(V)/Pi transporters[35]. Significant changes in the expression profile of 14-3-3 protein family in response to As stress in AMF-colonized rice were demonstrated by Pathare *et al.*[36]. The expression of *OsGF14c*, *OsGF14e* and *OsGF14g* genes had significantly declined after one day of As treatment, while at three days of As stress, maximum downregulation of expression was shown by *OsGF14a*, followed by *OsGF14b*, *OsGF14h*, *OsGF14c* and *OsGF14d*, revealing that the impact of As stress on the expression is time-dependent. As treatment significantly increased the expression of the genes *OsASA2* and *OsYUCCA2* while

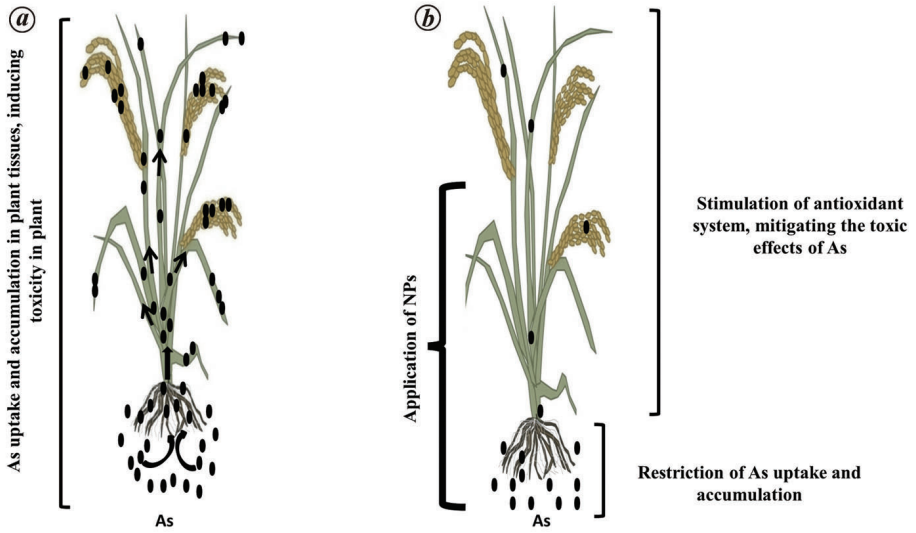

Figure 2. Mitigation of arsenic stress in plants with the application of nanoparticles (NPs). ***a***, Arsenic induced toxicity with its accumulation in different tissues. ***b***, Restriction of As uptake and activation of antioxidant defence mechanism by NPs, thereby mitigating As stress in plants.

inhibiting the expression of the IAA influx carrier *AUX1* and efflux carrier *PIN5* (ref. 17). As stress also altered the expression of nitrogen absorption and assimilation-related genes in rice plant. The expression of genes *NR*, *NiR* and GOGAT was downregulated under As treatment in both roots and shoots with respect to control, while the expression of *NiR*, *NRT2* and *AMT1* genes was found to be upregulated in roots and downregulated in shoots under As stress[37].

Nanoparticles for the mitigation of arsenic

Mitigation of As stress in plants is one of the important challenges to ensure food security. Plants adopt important mechanisms to combat stress, such as restriction of As uptake and stimulation of antioxidant defence system. It has been observed from various studies that NPs restrict As uptake with the increase in nutrient intake and antioxidant activity, thereby mitigating As stress in plants. The antioxidant defence system is found to be the prominent mechanism to cope with As stress[10,11,38].

Alleviation of heavy metal stress in different plants by NPs through acting as a source of essential elements, absorption of toxic heavy metals and increase in antioxidant enzymes, thereby reducing the accumulation of ROS and oxidative damage, has been recently reviewed by Zhou *et al.*[38]. Ahmad *et al.*[10] reported that application of zinc oxide NPs (ZnO NPs) ameliorates As toxicity in soybean plants by restricting As uptake and modulating the antioxidant enzymes, glyoxalase system and ascorbate–glutathione cycle. A similar observation of the ameliorating effects of ZnO NPs against As stress was reported in rice by reducing As uptake while enhancing zinc concentration, germination and growth of the plant[39,40]. The mitigating effect of iron oxide NPs (IO NPs) against As stress was reported by Mushtaq *et al.*[41], where the activity of peroxidase (POD) and superoxide dismutase (SOD) enzymes was found to be increased under IO NPs treatment in *Cucurbita moschata*, while reducing the levels of electrolyte leakage (EL), hydrogen peroxide (H_2O_2) and malondialdehyde (MDA). Exogenous application of Fe_3O_4 NPs augmented the antioxidant enzymes, protein content and photosynthetic pigments under As stress in the Indian mustard plant (*Brassica juncea*. L.)[42]. The authors revealed that the ability of Fe_3O_4 NPs to restrict the entry of As into the plant might lead to a decrease in the stress-related parameters[42]. They reported that IO NPs act as nano-adsorbents in the amelioration of As stress. The *Bacillus subtilus*-synthesized Fe_3O_4 NPs also act as nano-adsorbents in lowering the effect of As toxicity in rice plants and improving their growth[43]. Promising effects of NPs against arsenic stress in plant is shown in Figure 2.

Ti NPs have the potential to mitigate As stress by upregulating the expression of antioxidant genes[44]. Ti NPs, especially the green synthesized Ti NPs, confer tolerance to As-induced oxidative damage by augmenting the antioxidant machinery. Activation of plant antioxidant defence system by the application of Ti NPs was also reported by Salar *et al.*[45] in *Dracocephalum kotschyi* Boiss, where the antioxidant enzymes SOD, CAT and APX were significantly increased under Ti NPs treatment. Wu *et al.*[46] studied the effect of rutile nano-TiO_2 (NRT) in the amelioration of As stress in rice. They found that 1000 mg/l of rutile NRT reduced As uptake in exposed rice seedlings without causing significant oxidative stress in the plants. Accumulation of As in plants reduced by 40–90% with the application of NRT due to its strong sorption process. Si NPs augmented pectin synthesis and the mechanical force of the cell wall to inhibit the uptake of As into rice suspension cells[47].

Table 1. Mitigating effect of nanoparticles (NPs) against arsenic (As) and other heavy metals stress in plants

Concentration	Duration of treatment	Plant type	Effects	NPs	Mitigating effects	Reference
10 and 20 µM As	60 days	Soybean	Inhibits growth and induces oxidative stress	ZnO NPs	Increases enzymes involved in the ascorbate – glutathione cycle, including SOD, CAT, APX and GR	10
6.76 mg/kg As	45 days	Rice	–	ZnO NPs (100 mg/kg)	Lowers As accumulation	39
10, 20 and 30 mg/l As	60 days	*Cucurbita moschata*	Oxidative stress	IO NPs (5, 10, 15 and 20 mg/l	Increases activity of antioxidant enzymes	41
150 µM As	96 h	Indian mustard	Inhibits germination and growth and induces oxidative stress	Fe_3O_4 NPs (500 mg/l Fe_3O_4)	Restricts entry of As and stimulates antioxidant enzymes	42
5, 10 and 15 ppm As	14 days	Rice	Inhibits germination and growth of seedlings	Fe_3O_4 NPs (5 ppm)	Restricts As uptake	43
10 mM As	5 days	*Vigna radiata* L.	Exaggeration of reactive oxygen species (ROS) production leading to oxidative stress	TiNPs (0.1%)	Inhibits As uptake and reduces ROS level by augmenting the antioxidant machinery	44
10, 20, 40 and 80 µM As	24 h	Rice	Causes oxidative damage and destroys cell integrity	SiO_2 NPs (0.1 and 1 mM)	Inhibits As uptake and transport, and significantly decreases As-induced oxidative stress	47
4.23 mg/kg Cd	80 days	Wheat	Causes oxidative stress	Fe NPs (25, 50 and 100 mg/kg)	Inhibits Cd uptake and enhances Fe content	49
10 mg/kg Cd	30 days	Rice	Induces oxidative stress and inhibits plant growth	IO NPs and HG NPs (25, 50, 100 mg/kg)	Increases nutrient and antioxidant contents	56
7.86 mg/kg (total) and 1.32 mg/kg (available) Cd	55 days	Rice	Affects growth and photosynthesis	Fe NPs (10, 20, 30 mg/l)	Significantly decreases Cd intake	57
0.93 mg/kg Cd	80 days	Wheat	Reduces growth and induces oxidative stress	ZnO NPs (25, 50, 75 and 100 mg l^{-1})	Reduces Cd concentration, while increases Zn concentration and antioxidant enzymes	58
50 µM Cd	14 days	Rice	Induces oxidative stress	CeO_2 NPs (200 mg/l)	Triggers the antioxidant defence systems	59
7.86 mg/kg Cd	75 days	Maize	Causes oxidative stress	ZnO NPs (50, 75, 100 mg/l)	Reduces Cd and Zn concentration and increases antioxidant enzymes activities	60
1.21 mg/kg Cd	80 days	Wheat	Inhibits growth and photosynthesis and induces oxidative stress	Si NPs (25, 50 and 100 mg/kg)	Counteracts oxidative stress with increases in antioxidant enzymes	61
12 and 25 mg/kg Al	21 days	Maize	Inhibits growth and photosynthesis and induces oxidative stress	Silicon dioxide nanoparticles (SNPs) (4 mg/kg)	Improves ROS scavenging system by activating antioxidant contents and activities	62

This work reveals the mechanism of inhibiting As uptake into the rice at the single-cell level by SiO_2 (ref. 47). By treatment with SiO_2 NPs, pectin methylesterase (PME) activity, cation exchange capacity (CEC), pectin content and cell thickness had increased, thus maintaining the integrity of the cell undergoing As stress. It also improved the mechanical force of the cell wall by decreasing the degree of pectin methylesterification in rice. The SiO_2 NPs treated cells showed higher expression of OsNIP1; 1 and OsNIP3; 3 and lower expression of *OsLis1* and *OsLis2* genes. These findings indicate the possibility of using SiO_2 NPs in As-contaminated paddy soil. It has been reported that many other abiotic stresses such as salinity stress, drought and Cd stress were mitigated using different NPs by increasing antioxidant enzyme activity while lowering ROS[48,49]. The recent study by Hussain *et al.*[50] on the use of different NPs (ZnO, FeO and Si) under Cd stress in wheat plants also revealed that NPs ameliorate Cd stress by increasing nutrient uptake and antioxidant enzyme activity, while reducing Cd intake by the plant. The potential of NPs to mitigate abiotic stress in crop plants was reviewed by Das and Das[51], where the significant role of NPs in mediating different stresses has been explained. Abiotic stress such as drought, flood or salinity stress can be mediated by different NPs, including Ag, Al_2O_3, Fe_3O_4, TiO_2, SiO_2 and ZnO in different plants by increasing the essential nutrients content, and enzymic and non-enzymic antioxidants, thus increasing the total antioxidant capacity of the plant. Studies have also demonstrated the stimulation of antioxidant enzymes with supplementation of NPs, enhancing plant defence system and tolerance against salt, drought and cold stress[48,52,53]. NPs possess great potential for ameliorating different stresses by counteracting stress-induced oxidative damage with an increase in antioxidant activity. Khan *et al.*[54] and Praveen *et al.*[55] also showed the prominent role of antioxidants in the mitigation of As in plants. Table 1 shows mitigating effects of NPs against arsenic and other heavy metals stress in plants.

Conclusion and future perspectives

One of the major problems facing the world today is to achieve food security for the growing population, which fundamentally depends on agriculture. However, agricultural production is hindered by many factors, of which As stress causes a significant reduction in plant growth and yield. However, as described in this article, the impact of As stress can be mitigated by NPs with the stimulation of plant defence mechanisms. NPs restrict the uptake of As while enhancing nutrient content. Moreover, NPs improve the antioxidant system, which strictly regulates ROS concentration preventing oxidative stress in plants. Thus NPs can be a promising tool for mitigating As stress in plants. However, the effect of NPs is highly dependent on the concentration of NPs applied. Therefore, it is essential to determine the effective concentration of NPs for the successful mitigation of As stress. Since As uptake is regulated by different transporters, we must understand the different transporters involved for better uptake restriction and how NPs can influence these transporters to restrict the uptake of As, while enhancing essential elements. Therefore, future research needs to focus on NPs in the plant antioxidant system and transporters for better results in mitigating As stress in plants, which could achieve food security.

1. Abbas, G., Murtaza, B., Bibi, I., Shahid, M., Niazi, N. K., Khan, M. I. and Hussain, M., Arsenic uptake, toxicity, detoxification, and speciation in plants: physiological, biochemical, and molecular aspects. *Int. J. Environ. Res. Public Health*, 2018, **15**(1), 59.
2. Thounaojam, T. C., Khan, Z. and Upadhyaya, H., Molecular physiology of arsenic uptake, transport, and metabolism in rice. In *Arsenic in Drinking Water and Food*, Springer, Singapore, 2020, pp. 391–410.
3. Pan, W., Wu, C., Xue, S. and Hartley, W., Arsenic dynamics in the rhizosphere and its sequestration on rice roots as affected by root oxidation. *J. Environ. Sci*., 2014, **26**(4), 892–899.
4. Sohn, E., Contamination: the toxic side of rice. *Nature*, 2014, **514**(7524), S62–S63.
5. Majumder, B., Das, S., Mukhopadhyay, S. and Biswas, A. K., Identification of arsenic-tolerant and arsenic-sensitive rice (*Oryza sativa* L.) cultivars on the basis of arsenic accumulation assisted stress perception, morpho-biochemical responses, and alteration in genomic template stability. *Protoplasma*, 2019, **256**(1), 193–211.
6. Siddiqui, F., Tandon, P. K. and Srivastava, S., Arsenite and arsenate impact the oxidative status and antioxidant responses in *Ocimum tenuiflorum* L. *Physiol. Mol. Biol. Plants*, 2015, **21**(3), 453–458.
7. Rahman, A., Mostofa, M. G., Alam, M., Nahar, K., Hasanuzzaman, M. and Fujita, M., Calcium mitigates arsenic toxicity in rice seedlings by reducing arsenic uptake and modulating the antioxidant defense and glyoxalase systems and stress markers. *Biomed Res. Int.*, 2015, **340812**, 1–12.
8. Souri, Z., Karimi, N. and de Oliveira, L. M., Antioxidant enzymes responses in shoots of arsenic hyperaccumulator, *Isatis cappadocica* Desv. under interaction of arsenate and phosphate. *Environ. Technol.*, 2018, **39**(10), 1316–1327.
9. Li, J., Zhao, Q., Xue, B., Wu, H., Song, G. and Zhang, X., Arsenic and nutrient absorption characteristics and antioxidant response in different leaves of two ryegrass (*Lolium perenne*) species under arsenic stress. *PLoS ONE*, 2019, **14**(11), e0225373.
10. Ahmad, P. *et al.*, Zinc oxide nanoparticles application alleviates arsenic (As) toxicity in soybean plants by restricting the uptake of As and modulating key biochemical attributes, antioxidant enzymes, ascorbate–glutathione cycle and glyoxalase system. *Plants*, 2020, **9**, 825.
11. Bidi, H., Fallah, H., Niknejad, Y. and Tari, D. B., Iron oxide nanoparticles alleviate arsenic phytotoxicity in rice by improving iron uptake, oxidative stress tolerance and diminishing arsenic accumulation. *Plant Physiol. Biochem.*, 2021, **163**, 348–357.
12. Niazi, N. K. *et al.*, Phosphate-assisted phytoremediation of arsenic by *Brassica napus* and *Brassica juncea*: morphological and physiological response. *Int. J. Phytoremed*., 2017, **19**(7), 670–678.
13. Singh, H. P., Batish, D. R., Kohli, R. K. and Arora, K., Arsenic-induced root growth inhibition in mung bean (*Phaseolus aureus* Roxb.) is due to oxidative stress resulting from enhanced lipid peroxidation. *Plant Growth Regul*., 2007, **53**(1), 65–73.
14. Nath, S., Panda, P., Mishra, S., Dey, M., Choudhury, S., Sahoo, L. and Panda, S. K., Arsenic stress in rice: redox consequences and regulation by iron. *Plant Physiol. Biochem*., 2014, **80**, 203–210.
15. Thounaojam, T. C., Meetei, T. T., Panda, S. K. and Upadhyaya, H., North East India rice genotypes: screening of arsenic tolerant and

sensitive rice at germinating stage. *J. Stress Physiol. Biochem.*, 2019, **15**(4).
16. Sharma, P., Goyal, K., Kumar, T. and Chauhan, N. S., Inimical effects of arsenic on the plant physiology and possible biotechnological solutions to mitigate arsenic-induced toxicity. In *Contaminants in Agriculture*, Springer, Cham, Switzerland, 2020, pp. 399–422.
17. Ronzan, M., Piacentini, D., Fattorini, L., Della Rovere, F., Eiche, E., Riemann, M. and Falasca, G., Cadmium and arsenic affect root development in *Oryza sativa* L. negatively interacting with auxin. *Environ. Exp. Bot.*, 2018, **151**, 64–75.
18. Atabaki, N., Shaharuddin, N. A., Ahmad, S. A., Nulit, R. and Abiri, R., Assessment of water mimosa (*Neptunia oleracea* Lour.) morphological, physiological, and removal efficiency for phytoremediation of arsenic-polluted water. *Plants*, 2020, **9**(11), 1500.
19. Hu, Y. *et al.*, The role of reactive oxygen species in arsenic toxicity. *Biomolecules*, 2020, **10**(2), 240.
20. Meharg, A. A. and Hartley-Whitaker, J., Arsenic uptake and metabolism in arsenic resistant and nonresistant plant species. *New Phytol*., 2002, **154**(1), 29–43.
21. Sudhani, H. P., García-Murria, M. J. and Moreno, J., Reversible inhibition of CO_2 fixation by ribulose 1,5-bisphosphate carboxylase/oxygenase through the synergic effect of arsenite and a monothiol. *Plant Cell Environ*., 2013, **36**(6), 1160–1170.
22. Bergquist, E. R., Fischer, R. J., Sugden, K. D. and Martin, B. D., Inhibition by methylated organoarsenicals of the respiratory 2-oxo-acid dehydrogenases. *J. Organomet. Chem*., 2009, **694**(6), 973–980.
23. Gusman, G. S., Oliveira, J. A., Farnese, F. S. and Cambraia, J., Arsenate and arsenite: the toxic effects on photosynthesis and growth of lettuce plants. *Acta Physiol. Plant*., 2013, **35**(4), 1201–1209.
24. Shahid, M. A. *et al.*, Selenium impedes cadmium and arsenic toxicity in potato by modulating carbohydrate and nitrogen metabolism. *Ecotoxicol. Environ. Saf*., 2019, **180**, 588–599.
25. Pavlíkova, D., Zemanova, V., Pavlik, M., Dobrev, P. I., Hnilicka, F. and Motyka, V., Response of cytokinins and nitrogen metabolism in the fronds of *Pteris* sp. under arsenic stress. *PLoS ONE*, 2020, **15**(5), e0233055.
26. Gresser, M. J., ADP-arsenate. Formation by submitochondrial particles under phosphorylating conditions. *J. Biol. Chem.*, 1981, **256**(12), 5981–5983.
27. Nemeti, B., Regonesi, M. E., Tortora, P. and Gregus, Z., The mechanism of the polynucleotide phosphorylase-catalyzed arsenolysis of ADP. *Biochimie*, 2011, **93**(3), 624–627.
28. Byers, L. D., She, H. S. and Alayoff, A., Interaction of phosphate analogs with glyceraldehyde-3-phosphate dehydrogenase. *Biochemistry*, 1979, **18**(12), 2471–2480.
29. Tariang, K. U., Ramanujam, S. N. and Das, B., Effect of arsenic (As) and lead (Pb) on glycogen content and on the activities of selected enzymes involved in carbohydrate metabolism in freshwater catfish, *Heteropneustes fossilis*. *Int. Aquat. Res*., 2019, **11**(3), 253–266.
30. Pandey, A. K., Gedda, M. R. and Verma, A. K., Effect of arsenic stress on expression pattern of a rice specific miR156j at various developmental stages and their allied co-expression target networks. *Front. Plant Sci*., 2020, **11**, 752.
31. Marotti, I., Betti, L., Bregola, V., Bosi, S., Trebbi, G., Borghini, G. and Dinelli, G., Transcriptome profiling of wheat seedlings following treatment with ultrahigh diluted arsenic trioxide. *Evid.-Based Complement. Altern. Med*., 2014, 851263.
32. Pan, D., Yi, J., Li, F., Li, X., Liu, C., Wu, W. and Tao, T., Dynamics of gene expression associated with arsenic uptake and transport in rice during the whole growth period. *BMC Plant Biol*., 2020, **20**, 1–10.
33. Chen, Y., Xu, W., Shen, H., Yan, H., Xu, W., He, Z. and Ma, M., Engineering arsenic tolerance and hyperaccumulation in plants for phytoremediation by a PvACR3 transgenic approach. *Environ. Sci. Technol*., 2013, **47**(16), 9355–9362.
34. Zvobgo, G., LwalabaWaLwalaba, J., Sagonda, T., Mapodzeke, J. M., Muhammad, N., Shamsi, I. H. and Zhang, G., Phosphate alleviates arsenate toxicity by altering expression of phosphate transporters in the tolerant barley genotypes. *Ecotoxicol. Environ. Saf*., 2018, **147**, 832–839.
35. Castrillo, G. *et al.*, WRKY6 transcription factor restricts arsenate uptake and transposon activation in *Arabidopsis*. *Plant Cell*, 2013, **25**(8), 2944–2957.
36. Pathare, V., Srivastava, S., Sonawane, B. V. and Suprasanna, P., Arsenic stress affects the expression profile of genes of 14-3-3 proteins in the shoot of mycorrhiza colonized rice. *Physiol. Mol. Biol. Plants*, 2016, **22**(4), 515–522.
37. Khan, E. and Gupta, M., Arsenic–silicon priming of rice (*Oryza sativa* L.) seeds influence mineral nutrient uptake and biochemical responses through modulation of Lsi-1, Lsi-2, Lsi-6 and nutrient transporter genes. *Sci. Rep*., 2018, **8**(1), 1–16.
38. Zhou, P. *et al.*, Application of nanoparticles alleviates heavy metals stress and promotes plant growth: An overview. *Nanomaterials*, 2021, **11**(1), 26.
39. Ma, X., Sharifan, H., Dou, F. and Sun, W., Simultaneous reduction of arsenic (As) and cadmium (Cd) accumulation in rice by zinc oxide nanoparticles. *Chem. Eng. J*., 2020, **384**, 123802.
40. Wu, F., Fang, Q., Yan, S., Pan, L., Tang, X. and Ye, W., Effects of zinc oxide nanoparticles on arsenic stress in rice (*Oryza sativa* L.): germination, early growth, and arsenic uptake. *Environ. Sci. Pollut. Res*., 2020, **27**, 26974–26981.
41. Mushtaq, T., Shah, A. A., Akram, W. and Yasin, N. A., Synergistic ameliorative effect of iron oxide nanoparticles and *Bacillus subtilis* S4 against arsenic toxicity in *Cucurbita moschata*: polyamines, antioxidants, and physiochemical studies. *Int. J. Phytoremediat.*, 2020, **22**, 1408–1419.
42. Praveen, A., Khan, E., Perwez, M., Sardar, M. and Gupta, M., Iron oxide nanoparticles as nano-adsorbents: a possible way to reduce arsenic phytotoxicity in Indian mustard plant (*Brassica juncea* L.). *J. Plant Growth Regul*., 2018, **37**, 612–624.
43. Khan, S., Akhtar, N., Rehman, S. U., Shujah, S., Rha, E. S. and Jamil, M., Biosynthesized iron oxide nanoparticles (Fe_3O_4 NPs) mitigate arsenic toxicity in rice seedlings. *Toxics*, 2021, **9**, 2.
44. Katiyar, P., Yadu, B., Korram, J., Satnami, M. L., Kumar, M. and Keshavkant, S., Titanium nanoparticles attenuates arsenic toxicity by up-regulating expressions of defensive genes in *Vigna radiata* L. *J. Environ. Sci*., 2020, **92**, 18–27.
45. Salar, E., Khavari-Nejad, R. A., Mandoulakani, B. A. and Najafi, F., Effects of TiO_2 nanoparticles on activity of antioxidant enzymes, the expression of genes involved in rosmarinic acid biosynthesis and rosmarinic acid content in *Dracocephalum kotschyi* Boiss. *Russ. J. Plant Physiol.*, 2021, **68**(1), 118–125.
46. Wu, X. *et al.*, Application of TiO_2 nanoparticles to reduce bioaccumulation of arsenic in rice seedlings (*Oryza sativa* L.): a mechanistic study. *J. Hazard. Mater.*, 2020, 124047.
47. Cui, J., Li, Y., Jin, Q. and Li, F., Silica nanoparticles inhibit arsenic uptake into rice suspension cells via improving pectin synthesis and the mechanical force of the cell wall. *Environ Sci.: Nano*, 2020, **7**, 162–171.
48. Gohari, G., Mohammadi, A., Akbari, A., Panahirad, S., Dadpour, M. R., Fotopoulos, V. and Kimura, S., Titanium dioxide nanoparticles (TiO_2 NPs) promote growth and ameliorate salinity stress effects on essential oil profile and biochemical attributes of *Dracocephalum moldavica*. *Sci. Rep.*, 2020, **10**(1), 1–14.
49. Adrees, M. *et al.*, Simultaneous mitigation of cadmium and drought stress in wheat by soil application of iron nanoparticles. *Chemosphere*, 2020, **238**, 124681.
50. Hussain, A. *et al.*, Combined use of different nanoparticles effectively decreased cadmium (Cd) concentration in grains of wheat grown in a field contaminated with Cd. *Ecotoxicol. Environ. Saf.*, 2020, **215**, 112139.
51. Das, A. and Das, B., Nanotechnology a potential tool to mitigate abiotic stress in crop plants. In *Abiotic and Biotic Stress in Plants*, IntechOpen, London, UK, 2019.

52. Duo, L. A., Liu, C. X. and Zhao, S. L., Alleviation of drought stress in turfgrass by the combined application of nano-compost and microbes from compost. *Russ. J. Plant Physiol*., 2018, **65**(3), 419–426.
53. Mohammadi, R., Maali-Amiri, R. and Mantri, N. L., Effect of TiO_2 nanoparticles on oxidative damage and antioxidant defense systems in chickpea seedlings during cold stress. *Russ. J. Plant Physiol*., 2014, **61**(6), 768–775.
54. Khan, M. I. R. *et al*., Crosstalk of plant growth regulators protects photosynthetic performance from arsenic damage by modulating defense systems in rice. *Ecotoxicol. Environ. Saf*., 2021, **222**, 112535.
55. Praveen, A., Pandey, C., Ehasanullah, K., Panthri, M. and Gupta, M., Silicon-mediated genotoxic alterations in *Brassica juncea* under arsenic stress: a comparative study of biochemical and molecular markers. *Pedosphere*, 2020, **30**, 517–527.
56. Ahmed, T. *et al.*, Nanoparticle-based amelioration of drought stress and cadmium toxicity in rice via triggering the stress responsive genetic mechanisms and nutrient acquisition. *Ecotoxicol. Environ. Saf.*, 2021, **209**, 111829.
57. Rizwan, M., Noureen, S., Ali, S., Anwar, S., Rehman, M. Z. U., Qayyum, M. F. and Hussain, A., Influence of biochar amendment and foliar application of iron oxide nanoparticles on growth, photosynthesis, and cadmium accumulation in rice biomass. *J. Soil. Sediment.*, 2019, **19**, 3749–3759.
58. Hussain, A. *et al.*, Zinc oxide nanoparticles alter the wheat physiological response and reduce the cadmium uptake by plants. *Environ. Pollut*., 2018, **242**, 1518–1526.
59. Wang, Y. *et al.*, Effects of cerium oxide on rice seedlings as affected by co-exposure of cadmium and salt. *Environ. Pollut.*, 2019, **252**, 1087–1096.
60. Rizwan, M. *et al.*, Alleviation of cadmium accumulation in maize (*Zea mays* L.) by foliar spray of zinc oxide nanoparticles and biochar to contaminated soil. *Environ. Pollut*., 2019, **248**, 358–367.
61. Khan, Z. S. *et al.*, Effects of silicon nanoparticles on growth and physiology of wheat in cadmium contaminated soil under different soil moisture levels. *Environ. Sci. Pollut. Res*., 2020, **27**, 4958–4968.
62. de Sousa, A. *et al.*, Silicon dioxide nanoparticles ameliorate the phytotoxic hazards of aluminum in maize grown on acidic soil. *Sci. Total Environ*., 2019, **693**, 133636.

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