ARSENIC UPTAKE AND ACCUMULATION IN PLANTS: TOXICITY AND ANTIOXIDANT DEFENCE SYSTEM

Akan Barhai*, Suchismita Das*

* Assam University, Department of Life Science and Bioinformatics, Aquatic Toxicology and Remediation Laboratory, Silchar, India

corresponding author: Suchismita Das, e-mail: drsuchismita9@gmail.com

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ABSTRACT

Arsenic uptake by plants is species-specific and its level in terrestrial plants of uncontaminated sites ranged from 0.009 to 1.5 mg/kg. Plants with high metal or metalloid uptake capability in their biomass are called hyperaccumulators. The most efficient arsenic (As) hyperaccumulator belongs to Pteridaceae with species *Pteris vittata* L. and *Pityrogramma calomelanos* L., both species can accumulate more than 8000 mg/kg As in their above-ground parts. Higher concentrations of As can interfere with various metabolic activities and manifest through several morphological impairments. A higher concentration of As accelerates the production of free radicals and reactive oxygen species (ROS) within the cell. Plants have a scavenging system to regulate the production of ROS; the scavenging system is also known as the antioxidant defence system. The defence mechanism consists of both an enzymatic and non-enzymatic antioxidant system. Non-enzymatic antioxidant includes carotenoids, ascorbic acid, and glutathione whereas the enzymatic antioxidant system comprises superoxide dismutase, catalase, ascorbate peroxidase, guaiacol peroxidase, and glutathione reductase.

Keywords: *arsenic in plants, physiological disturbances, reactive oxygen species, antioxidant enzymes*

INTRODUCTION

Plants depend on soil for their nutrients but there is no report that As is important for their growth and development. Plants take up As due to its chemical resemblance with phosphate (P) and which mostly inhibits the P uptake [1, 2]. In general, transport of As in plants is not very effective and most of the time it remains in the roots. However, by way of exception, some plants can effectively accumulate As into their aerial parts [3]. Arsenic uptake by terrestrial plants is largely species-specific and shows a positive relationship between As concentration in plants tissue and soil, but paradoxically a study demonstrated a lower concentration of As in plants tissue instead of a high concentration in soil. Plants take up As (V) via P transporters, while As (III) is taken up through aquaporins. Once inside the plant, a minute concentration As is translocated to the

shoots via the xylem as oxyanions and dimethyl arsenic [4, 5]. An estimated amount of As in plants growing in terrestrial and uncontaminated soil ranged from 0.009 to 1.5 mg/kg based on dry weight [6, 7]. Some plants that grow in the metal-containing environment have evolved themselves to tolerate and take up a higher amount of As in their tissue without any toxicity symptoms. Plants that have the potential to uptake and accumulate a high amount of metals or metalloids are called hyperaccumulators. It is estimated that hyperaccumulators have the potential to accumulate > 1000 mg/kg of As in their tissue [8 - 10]. The most efficient As hyperaccumulator belongs to Pteridaceae with species *Pteris vittata* L. and *Pityrogramma calomelanos* L.; both species can accumulate more than 8000 mg/kg of As in the above-ground tissue. There are other plants species, excluding ferns, such as *Melastoma malabrathricum* L., *Mimosa pudica* L., *Hydrilla verticillata* L., *Portulaca oleracea* L., *P. tuberosa* Roxb., *Eclipta alba* L., and *Limnanthes spp.* [11 - 13]. The most present arsenic compounds in plants are arsenite (As (III)) and arsenate (As (V)). However, a few species may contain a trace amount of MMA (monomethyl arsenic) and DMA (dimethyl arsenic). The capability of plants to absorb elements from their surroundings and trans-locate them to their aerial parts mainly depends on soil properties, pH, organic matters, redox potential, microbial activities, and availability of iron oxides [14 - 16]. Plants use three separate As uptake pathways: (1) direct transport from the environment to the plant vascular system, (2) passive uptake through the apoplast, and, (3) active uptake through the symplast. Once the As is taken up by the plants, a small concentration is translocated to their aerial parts and the order of concentration gradient is: roots > stems > leaves [17, 18]. In this review, we summarized the As uptake pathways and translocation mechanism in plants. This review further explained the toxic effects of As in plants and their antioxidant defence mechanisms.

TOXICITY OF As IN PLANTS

Arsenic is a non-essential metalloid for plants and does not involve any metabolic processes when supplied at a low concentration. However, at a higher level, As can inhibit various metabolic activities and manifest through several morphological changes such as violet leaf colour, leaf necrosis, leaves wilting, decrease in shoot and root length, decrease or complete damage of root hairs, damage of thylakoid membrane, impairment of epithelial cell and cortex and eventually leads to cell death [19, 20]. Some other anatomical changes resulting from As toxicity are necrosis, reduced pith differentiation, and a decrease in the root branching system. Furthermore, As-induced toxic effects in plants physiology include reduction in the plants growth, gas exchange through leaves, water potential, nutrients supply, protein content, inhibition of chlorophyll synthesis, phytase activity, decrease in the photosynthetic productivity of plants, and biomass accumulation [21]. Arsenic can reduce a plant's reproductive capability by affecting its reproductive organs and fertility rate resulting in low yield or fruit production [22]. The toxicity of As mainly depends on the arsenic compound supplied to the plants. As(V) is rapidly accumulated by plant roots through the phosphate uptake pathway, while As(III) is taken up by aquaporin and reacts with sulfhydryl groups downregulating catalytic functions [23 - 25]. Arsenic (V) mainly affects primary and secondary metabolism, cell wall rigidity, seedling germination, and abscisic acid metabolism. Arsenic (III) particularly affects the signaling processes [26]. Arsenic may also interfere with the micro and macronutrient uptake because it competes with nutrients for transporters; for example, As(V) supply reduces the number of micronutrients [27].

REACTIVE OXYGEN SPECIES (ROS)

A plant's response to toxic metals is a complex process. Many heavy metals including As accelerate the production of free

radicals and ROS within the cell. ROS are the by-product of the respiratory and electron transport chain and other metabolic activities where huge electron flow occurs, like mitochondria and chloroplast. In addition, ROS can also be produced in the peroxisomes, plasma membrane, endoplasmic reticulum, and apoplast (Figure 1) [28 - 30].

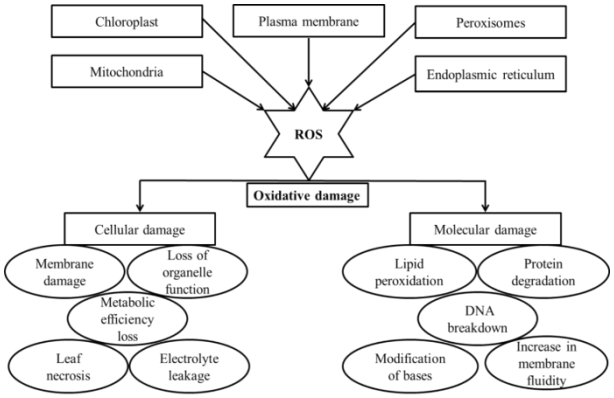

Figure 1. Production sites and damage caused by ROS

Arsenic generates ROS by suppressing major enzyme systems and electron leakage during the transformation of arsenate to arsenite. The ROS are extremely reactive, but in the normal environmental condition, these molecules are not capable of causing any damage as they are constantly being regulated by a variety of antioxidant enzymes. This delicate equilibrium between the formation of ROS and their antioxidant scavenging system can be disrupted by As stress (Figure 2) [31, 32]. Any disturbance in this equilibrium results in the overproduction of ROS which ultimately causes considerable cellular impairment [33]. ROS can be formed directly by ROS-active metals through the Haber-Weiss/Fenton reactions or by an indirect process by inducing reduced nicotinamide adenine dinucleotide phosphate (NADPH) oxidases. Another process of ROS production is by preventing enzymes through the replacement of necessary cations [34]. ROS comprises superoxide radical (O_2^{*-}), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and hydroxyl radicle ($^*OH$) [35].

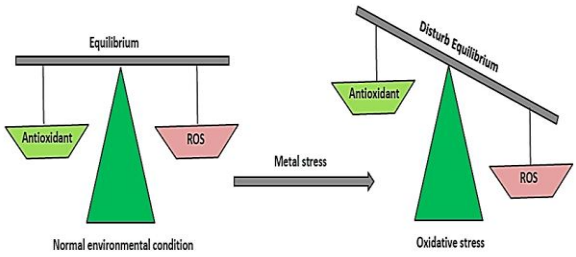

Figure 2. ROS activity in normal and stressed environmental conditions

Superoxide radicals are continuously produced throughout photosynthesis by partial reduction of O_2 molecules or transfer of energy to them within the chloroplast and other compartments of the cell. It is the first ROS produced inside the cell with very little reactive property and does not cause any extensive harm to the cells. But it can be transformed into more toxic and reactive forms such as $^*OH$ and $^1O_2$ [36 - 38].

Singlet oxygen is an uncommon form of ROS, not produced by transferring an electron to O_2. It is produced by reacting with the triplet form of chlorophyll in the antenna pigments of chloroplast with O_2. Singlet oxygen exerts a detrimental impact on both photosystem I (PSI) and photosystem II (PSII) resulting in risk to the entire photosynthetic mechanism [39]. $^1O_2$ may cause damage to a variety of biomolecules and pigments [40].

Hydrogen peroxide is mildly reactive and formed when O_2^{*-} undergoes protonation and univalent reduction. Mostly H_2O_2 is produced by a catalytic reaction with superoxide dismutase (SOD) or it can be produced non-enzymatically at low pH conditions. In plants, lower concentration of H_2O_2 is beneficial whereas a higher concentration causes damage to the cellular components. It causes a 50 % reduction in the various enzyme activity such as fructose 1,6, bisphosphatase and phosphoribulokinase. It also induces apoptosis at higher concentrations [41].

Hydroxyl radical is an extremely reactive form of ROS and it is produced in neutral pH by the Fenton reaction between H_2O_2 and O_2^{*-}. The reaction can also be catalysed by

transition metals, like Fe [42]. H_2O_2 has the potential to react with various biomolecules such as proteins, DNA, and lipids.

ANTIOXIDANT DEFENCE SYSTEM (ADS)

All the plants have a scavenging system to control the production of ROS; if this system does not adjust with the formation of ROS, the plants undergo oxidative stress. The scavenging systems are also known as the antioxidant defence system. Enzymes involved in this system are mostly electron donors which react with ROS and result in non-toxic neutral end products. The defence mechanism comprises both an enzymatic and non-enzymatic ADS (Figure 3). Non-enzymatic antioxidant includes carotenoids, ascorbic acid, and glutathione whereas the enzymatic ADS comprises superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and glutathione reductase (GR) [43].

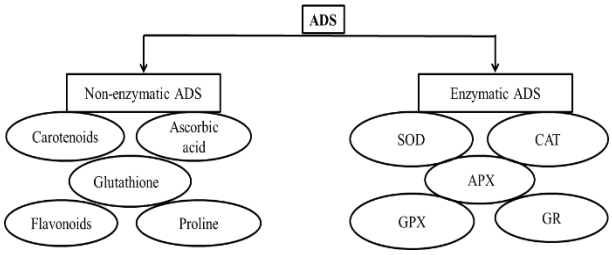

Figure 3. Enzymatic and non-enzymatic ADS

ENZYMATIC ANTIOXIDANTS

Superoxide dismutase (SOD)

SOD is found in all aerobic organisms and is a part of a group of metalloenzymes. Under stressful conditions, SOD act as the first line of defence against the damage triggered by ROS. It catalyses the elimination of O_2^{*-} by dismutating it into O_2 and H_2O_2 and reduces the threat of production of $^*OH$ by the Haber-Weiss reaction:

$$2O_2^- + 2H^+ \rightarrow O_2 + H_2O_2 \quad (1)$$

The primary site of SOD is the subcellular compartments where they produce activated oxygen which is susceptible to ROS-induced oxidative stress. Depending upon the metal cofactors, SODs are classified as manganese (Mn-SOD), copper/zinc (Cu/Zn-SOD), and iron (Fe-SOD). Mn-SOD is confined in mitochondria; Cu/Zn-SOD is in the chloroplast, cytosol, peroxisome, and Fe-SOD in the chloroplast [44].

Catalase (CAT)

CAT is a heme-containing enzyme and it was the first among all the antioxidant enzymes to be discovered and characterized. Plants consist of various H_2O_2-degrading enzymes, but CAT is different from others because it does not require a reducing agent. It catalyses the dismutation of H_2O_2 into H_2O and O_2. The affinity of CAT for H_2O_2 is higher as compared to organic peroxides (R-O-O-R). Productions of hydrogen peroxides are highest in the peroxisomes due to β-oxidation of fatty acids, purine catabolism, photorespiration, and oxidative stress.

$$2H_2O_2 \rightarrow 2H_2O + O_2 \quad (2)$$

Recently, CAT is also spotted in other cell organelles such as the mitochondria, chloroplast, cytosol [45]. When cells are under stress and rapidly produce H_2O_2 through catabolic processes, CAT degrades the H_2O_2 without consuming much energy [46]. The turnover number of CAT is considered as one of the highest, one molecule of CAT can degrade 26 million molecules of H_2O_2 into H_2O and O_2 per minute in a concentration-dependent manner [47].

Ascorbate peroxidase (APX)

Plants don't contain catalase in the chloroplast which is why plants have adopted an alternative mechanism to remove H_2O_2 by peroxidase through the ascorbate-glutathione

pathway. Ascorbate acts as a reducing agent to reduce hydrogen peroxide in water. Hence, peroxidase is also called APX. APX is a hemecontaining protein mainly found in some cyanobacteria and higher plants [48, 49]. They are also considered as one of the most common antioxidant enzymes in the plant system and consist of at least five isoforms based on different locations and amino acids including mitochondria, cytosol, chloroplastid (stromal and thylakoidal), and peroxisome. APX has a greater affinity for H_2O_2 as compared to CAT, which makes APXs better H_2O_2 scavengers under oxidative stress [50].

Guaiacol peroxidase (GPX)

GPX belongs to a large peroxidase family and is mostly found in the cytoplasm or cell wall-bound form. They play a significant role in the biosynthesis of lignin and degrade indole-3-acetic acid (IAA) to defend against various biotic stresses at expense of H_2O_2. Guaiacol and pyrogallol are the aromatic electron donors preferred by GPX and oxidize ascorbate at the rate of about 1 % that of guaiacol. GPX is extensively found in plants, animals, and microbes. There are various isoenzymes of GPX present in the plant cells and localized in the cytosol, vacuoles, and cell wall [51, 52].

Glutathione reductase (GR)

GR is a flavour-protein oxidoreductase present in both prokaryotes and eukaryotes. They use NADPH as a reductant to reduce oxidized glutathione to glutathione [53]. Glutathione plays a significant role in the cell system such as participation in the ascorbic acid and glutathione cycle, acting as a substrate for glutathione-S-transferase and maintaining the sulfhydryl (-SH) groups [54]. GR is mostly found in the chloroplasts, while a small amount is found in the mitochondria and cytosol. In the chloroplast, GR and glutathione take part in the detoxification of H_2O_2 produced by the Mehler reaction [55].

NON-ENZYMATIC ANTIOXIDANTS

Carotenoids

Carotenoids are lipid-soluble pigments generally found in plants and microorganisms. They are found in the thylakoid membrane of chloroplast and serve an important role in light-harvesting and antioxidant activity associated with the membrane. Plants have more than 600 carotenoids, which perform three main functions: (1) they absorb light of 400 - 500 nm and transfer it to chlorophyll [56], (2) act as a quencher of naturally produced triplet sensitizer (Chl3), O_2, and other damaging free radicals produced during photosynthesis [57] and (3) provide stability to light-harvesting complexes, thylakoid membranes and is significant for the PSI assembly [58].

Ascorbic acid (AA)

Ascorbic acid or vitamin C is the amplest and most extensively studied antioxidant present in the stroma of chloroplast, cytosol, apoplast, and vacuoles of the plant cell. The highest concentration of ascorbic acid is found in adult leaves with well-developed chlorophyll and chloroplast. It has the potential to contribute electrons in a vast number of reactions and because of that AA is categorized as the most powerful antioxidant. It also plays a substantial role in physiological processes, like metabolism, growth, and differentiation. In addition, AA is important for the elimination of H_2O_2 and regeneration of α-tocopherol and membrane-associated carotenoids through the ascorbate glutathione cycle. Components of the cycle have been reported in the mitochondria, cytoplasm, and peroxisome where it acts as ADS in these organelles [59 - 61].

Glutathione

Glutathione was detected in most of the cellular components such as chloroplast, cytosol, vacuoles, endoplasmic reticulum, and mitochondria. They are non-protein in nature

and play a significant role against ROS-induced oxidative damage. Glutathione has a reducing power, which is why it plays a vital role in several biological processes including signal transduction, enzymatic regulation, cell division and growth, synthesis of protein and nucleic acids, sulphate transport regulation, conjugation of metabolites, synthesis of phytochelatins, and expression of stress-responsive genes. It has the potential to act directly as a free radical scavenger because it can react with H_2O_2, O_2^{*-} and $^{*}OH$. It can also take part in the regeneration of another important antioxidant AA via the ascorbic acid-glutathione cycle [62].

CONCLUSION

From the above discussion, it can be concluded that the As uptake and its accumulation in plants adversely affect its biochemical and molecular activities. Arsenic can alter or inhibit the majority of physiological processes such as plants growth and photosynthetic efficiency. It can promote oxidative stress which results in the production of ROS and consequently damage proteins, lipids, and inhibits various metabolic pathways. The oxidative stress is diminished by the enhanced activities of various antioxidant enzymes such as SOD, CAT, APX, GPX, and GR.

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