

Beneficial Role of Metalloids in Plants: Molecular Understanding and Applicability



Priyanka Dhakate, Prateek Sharma, Sahil Mehta, Javed Akter, Vacha Bhatt, Sonali Chandanshive, Dhires Chakravarty, Mehzabin Rahman, and Md. Aminul Islam

1 Introduction

Metalloids are elements that have chemical properties between metals and non-metals. In the periodic table, metalloids are recognized as boron (B), silicon (Si), arsenic (As), germanium (Ge), antimony (Sb), tellurium (Te) and polonium (Po). These elements are placed diagonally between the metals and non-metals. Along with other elements, these metalloids are widely distributed in earth crust. Like many minerals, metalloids are known to regulate optimum growth and development of all animals and plants. However, it is also commonly known that enhanced metalloid concentration negatively impacts plant health by interfering in various

P. Dhakate · M. A. Islam (✉)

National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi, India

P. Sharma

Department of Biology, University of North Carolina, Chapel Hill, NC, USA

CSIR-National Botanical Research Institute (CSIR-NBRI), Rana Pratap Marg, Lucknow, India

S. Mehta

Crop Improvement Group, International Centre for Genetic Engineering and Biotechnology, Aruna Asaf Ali Marg, New Delhi, India

J. Akter

Soybean Research Institute, Nanjing Agricultural University, Nanjing, People's Republic of China

V. Bhatt · S. Chandanshive

Department of Botany, Savitribai Phule Pune University, Pune, India

D. Chakravarty

Department of Chemistry, Bimala Prasad Chaliha College, Nagarbera, Assam, India

M. Rahman

Advanced IBT Hub, Bimala Prasad Chaliha College, Nagarbera, Assam, India

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biochemical, structural and physiological processes of plant metabolism (Nagajyoti et al. 2010; Adrees et al. 2015; Afshan et al. 2015). These effects may range from substitution of essential functional groups to production of reactive oxygen species (ROS) and cellular damage (Anjum et al. 2015). Additionally, increased concentration of metalloids has been found to adversely affect plant biomass, growth, photosynthesis, accumulation and **translocation** of essential elements (Wagner 1993; Adrees et al. 2015). Consequently, extensive research into metalloid accumulation and resistance has been taken up across the globe in the last two decades to assess their immediate and long-term impact on environmental, human, livestock and plant health to optimize their bioavailability and uptake by plants to aid plant growth and yield (Nascimento and Xing 2006; Adrees et al. 2015). Compared to other organisms, plants are better equipped with strategies to withstand influx of metalloids and also regulate their metabolism to not affect their survival and reproductive success. Plant genes encode expanded gene families of transporters that regulate uptake and subsequent sequestration of metalloids. These transporters have specific substrate specificities, expression and localization on cellular membranes as they manage translocation of respective metalloids across the whole plant (Hwang et al. 2016). Analysis of these transporters has been conducted in numerous plant systems and their relevance has been assessed using several forward and reverse genetic approaches. Only a few metalloids such as boron, silicon and selenium have been studied extensively and are now well established to play beneficial roles in plant growth and metabolism. These beneficial metalloids serve as essential micronutrients and ensure optimum plant growth, development and productivity (Peterson et al. 1981). At optimum concentrations, metalloids effectively regulate function of many enzymes and metabolic pathways. Furthermore, these metalloids are instrumental in various biosynthetic pathways such as nucleic acid, chloroplast and protein besides governing structural and functional integrity of cellular membranes (Adrees et al. 2015; Oves et al. 2016). Therefore, in this chapter we discuss such incidences of metalloid relevance to plants, mechanisms of their transport and uptake, essential transporters, and various forward and reverse genetic approaches adapted to assay and optimize uptake of metalloids in plants.

2 Sources of Metalloid Ions

Presence of metalloids in soil is a combined result of various anthropogenic and natural processes. Most common source of natural metalloid contribution to the soil in question is rock substratum and geological bedrock (Tchounwou et al. 2012). The amount and composition of metalloids in the parent bedrock and weathering conditions determine concentration of metalloids in the resultant soil (Wuana and Okieimen 2011). Agriculture is another major source of metalloid contamination. Typically, all soils more or less have all known metalloids. However, their concentration varies; while some metalloids are found below the detection limit, some may be present at toxic amounts (Alloway 2013). Accordingly, the concentration of the

metalloids can be categorized as 'total' and 'available'. The 'available' metalloids constitute only a part of the 'total' concentration of metalloids present in the soil at a given time. Total concentration refers to presence of all forms of element in the soil such as adsorbed to minerals like clay, bound to organic matter, bound in crystal structure of minerals, carbonates, oxides, soluble organic and inorganic complexes in soil solution, and free ions. More often than not, only a fraction of this 'total' concentration is available for immediate uptake by plants. This 'available' concentration of the element is present in soil as soluble complexes, free ions or readily amenable forms. Further, this availability of the element to the plant is governed by many soil factors such as redox status, pH, temperature, macronutrients and water content. Additionally, plants are known to produce root exudates that can also significantly affect the availability of the metalloids. Assessing total concentration of a given metalloid is not a good indicator of the bioavailability of the element, notwithstanding these measures do indicate presence of anomalously increased or decreased concentrations of the metalloids. Such a measure is instrumental in assessing the effect on soil flora and fauna. Low levels of an element indicate that either the soil is derived from a bedrock that was deficient in the said element or the soil has become depleted over the years. In either case, such soils need to be supplemented with essential metalloids to ensure their bioavailability to growing plants.

3 Molecular Interactions During Plant Elemental Uptake

Essential metalloids required for plant growth and development are taken up primarily from the soil. To ensure regulated uptake of required metalloids (B, Si and Se), specific transporters and signalling mechanisms are in place. Such metalloids that are beneficial to several biochemical and physiological processes in plant growth are components of various cellular enzymes and regulate various oxidation–reduction reactions (Adrees et al. 2015; Emamverdian et al. 2015). Boron (B) is a vital element to numerous processes in plant development such as protein and amino acid (AA) biosynthesis, seed germination, nucleic acid metabolism, carbohydrate transportation, cell division and elongation, cell membrane integrity, sugar translocation, biosynthesis and transport of plant hormones, phenolic metabolism, gas exchange and water uptake (Kouchi and Kumazawa 1976; Camacho-Cristóbal et al. 2008; Han et al. 2008; Jehangir et al. 2017; Lu et al. 2015). High-affinity transport systems ensure boron uptake, accumulation and absorption in plants occur via specific boron transporters and chelators (Jehangir et al. 2017; Lu et al. 2015). Selenium (Se) is an essential element for plant growth owing to its antioxidant capacities. It has been established as a component of selenoenzymes such as thioredoxin reductases (TR) and glutathione peroxidase (GSH-Px). In addition, its availability is cardinal to optimum functioning of the enzymes that maintain the redox potential of the cell (Rayman 2000). Silicon (Si) plays a central role in important physiological processes of the plants such as transpiration and photosynthesis. Si is also central in conferring plants with adaptive capacities to tide over drought

conditions (Tubana et al. 2016). These essential and/or non-essential metalloids are absorbed from the soil in accordance to a concentration gradient that favours selective uptake of a certain ion over the other at a given time (Peralta-Videa et al. 2009). First step towards uptake is exploration of soil by root system for availability of the micronutrients. Root responses to explore macronutrients such as nitrogen (N) and phosphorus (P) are well established. However, root responses to metalloid deficiencies do not remain well characterized. In response to nutrient deficiency, plant tends to increase the surface area of roots by promoting branching of roots. Such incidences in root development have been noted in response to Fe deficiency in both monocots and dicots plants (Moog et al. 1995; Schmidt 2002). Second parameter that determines metalloid availability by roots is their bioavailability (Palmgren et al. 2008). Metalloids are present adsorbed to soil particles or in an insoluble form. Plant roots ensure to increase their bioavailability by uptake of specific transporters by changing them into appropriate forms by interacting with the surrounding rhizosphere (Marschner 1995; Palmer and Guerinot 2009). Plant roots exude acidification of the rhizosphere to generate a high membrane potential that drives cation uptake (Palmgren 2001). Additionally, protons that are released participate in cation exchange to release divalent metal ions that are bound to soil particles and consequently the acidification of rhizosphere releases metals from hydroxides (Palmer and Guerinot 2009; Palmgren 2001). Post mineral uptake, minerals migrate to apoplastic spaces from where metals are actively transported across plasma membrane into symplastic pathways.

Uptake of boron from soil and its subsequent transport to shoots is now explained using a model that has been developed based on available data from various different plant systems so far (Takano et al. 2008; Miwa and Fujiwara 2010; Durbak et al. 2014; Baxter and Dilkes 2012). According to this model, boron diffuses from the soil to the apoplast of root epidermis. The influx proteins present on the plasma membrane of the epidermis, endodermis and cortex transport boron to the cytosol. Boron then reaches the pericycle through the symplastic pathways, and efflux proteins subsequently load it into xylem vessels that ensure its availability across the plant system (Kohl and Oertli 1961). Uptake of silicon from soil occurs in the form of silicic acid (Takahashi and Hino 1978; Mitani et al. 2005). Three distinct models from Si uptake have been proposed in plants having varying concentration of Si accumulation and uptake (Takahashi et al. 1990). These models primarily profess active, passive and rejective mode of Si uptake. During passive uptake of Si the rate is similar to that of water uptake resulting decreased concentration of Si in the uptake solution. However, during rejective mode of Si uptake the Si concentration in uptake solution increases. These models have been found valid in a few plant systems. However, these mechanisms remain largely uncharacterized in plant systems so far. Selenium (Se) uptake in plants also varies between different plant species. Additionally, Se uptake is dependent on phases of plant development, soil conditions (salinity and pH) and concentration of Se (Renkema et al. 2012; Gupta and Gupta 2016). Se is present in two forms: selenate in alkaline soils and selenite in acidic soils (Gupta and Gupta 2016). Both of these forms have differential

absorption and mobility (Li et al. 2008). Selenate (SeO_4^{2-}) is the most prevalent and available form of Se (Missana et al. 2009; Gupta and Gupta 2016). In order of preference selenate is absorbed first in plants followed by selenomethionine (SeMet) and selenite. In plants, transporters in root cell membrane play an important role. While selenite is transported by phosphate transport mechanism (Zhang et al. 2014a), selenate uptake is mediated by sulphate transporters and channels (Feist and Parker 2008; Li et al. 2008; Zhang et al. 2003). Although high-affinity transport systems are cardinal for regulated plant growth and development, during the period of excess metal concentration in soil unspecific uptake of metal is unavoidable. For example, arsenic (As) is a metalloid with no established biological function in higher plants; therefore, no specific uptake mechanisms for these metals are in place. However, in soils with high As concentration, uptake of As occurs via phosphate transporters as As(V) that is reduced in plants to As(III) (Meharg Andrew and Hartley-Whitaker 2002). In reducing environments, aquaporin nodulin-26-like intrinsic proteins bind to As (III) (Bienert et al. 2008; Isayenkov and Maathuis 2008).

4 Beneficial Role of Metalloids in Plants

4.1 Boron

Boron (B) a trace element, a non-metal, is one of the eight essential micronutrients that are required by plant for their optimum growth and development. Maze (1919) was the first to recognize boron as an essential element for optimum plant growth of maize (*Zea mays* L.) plants. Warington (1923) illuminated relevance of boron in the development of broad bean (*Vicia faba* L.). Following this, Brenchley and Waeikngton (1927) displayed significance of boron in plant growth in different plant species. By the 1930s, boron was well recognized as an essential micronutrient for plants. Plants growing in soil that are deficient in boron concentration were found to have reduced crop yields and compromised crop quality. Boron requirement varies significantly across all plant species. For example, while corn requires increased boron concentrations, gramineae requires much lower amount. Decreased boron availability causes some of the most noted disorders in plants such as cracked stems of celery *Apium graveolens* L., brown heart of *Brassica napobrassica* Mill. and *Raphanus sativus* L. roots, brown heart of *Brassica oleracea* var. *botrytis* L., internal brown spots of *Ipomoea batatas* Lam. and heart rot of *Beta vulgaris* L. (Gupta and Gupta 2016). Boron is essential in regulating cell elongation and division, as a result of which it directly impacts root growth (Shelp 1993). Boron deficiency was found to have an adverse effect on root length elongation. It was found that root elongation in seedlings of *Cucurbita pepo* L. reduced within 3 h of removing boron supply and completely stopped within 24 h. However, restoring boron supply within 12 h restored root length elongation within 12–18 h (Bohnsack and Albert 1977). In *Helianthus*

annus L. presence of boron in soil resulted in development of adventitious roots (Josten and Kutschera 1999). Further it was found that in contaminated soils that have increased aluminium content and are acidic, application of boron prevented aluminium-mediated inhibition of root growth (Lenoble et al. 1996).

In boron-deficient soils, protein synthesis has been reported severely affected (Carpena Artes and Carpena Ruiz 1983). However, in such studies various parameters such as age of the plant, stage of organ development, localization and remobilization of proteins have not been taken into consideration (Shelp 1988). For example, growing bean (*Phaseolus vulgaris* L.) cotyledons without boron for 5 days increased protein concentration in comparison to control plants suggesting hindrance of nitrogen remobilization due to boron deficiency (Dave and Kannan 1981). However, protein concentrations in actively growing regions was found to slow down in incidences of boron deficiency (Duggar 1983; Shelp 1993). Partitioning of nitrogen into soluble components such as ammonium, nitrate and amino acids was found boron dependent in *Brassica oleracea* var. *botrytis* L. This, in turn, was found dependent on plant organ under study and concentration and duration of boron supply (Shelp 1993). Relative amino acid composition was not found affected due to boron deficiency. Inorganic nitrogen in plant tissues and translocation fluids was substantially increased. Boron deficiency increased nitrate reductase activity in *Beta vulgaris* L., *Lycopersicon esculentum* Mill., sunflower and corn (Bonilla et al. 1997; Kastori and Petrović 1989). In *Nicotiana tabacum* L., boron deficiency resulted in decreased leaf nitrogen and also resulted in decreased nitrate reductase activity (Camacho-Cristóbal et al. 2008). Boron-deficient plants *Glycine max* Merr. showed low acetyls reduction activities and damaged root nodules (Yamagishi and Yamamoto 1994). In *Vigna unguiculata* Walp, acute boron deficiency resulted in increased amounts of reducing and non-reducing sugar concentrations and at the same time decreased starch phosphorylase activity (Chatterjee et al. 1990). Boron deficiency has been documented to result in increased accumulation of phenolic substances as a result of upregulation of genes responsible for pentose phosphate shunt (Hajiboland and Farhanghi 2010). Foliar spray of boron to sunflower displayed increased accumulation of non-reducing sugars and starch concentrations (Shehzad et al. 2016). Such findings suggest a specific role of boron in the production and accumulation of starch and sugar reserves in sunflower seeds. Similar instances of increased accumulation of non-reducing sugars and starch were also found in *Brassica nigra* Koch (Sinha et al. 2000) and *Nicotiana tabacum* (Camacho-Cristóbal and González-Fontes 1999), respectively. In leaves of boron-deficient plants of *Pisum sativum* L., concentration of both starch and sugars increased. However, a marked decrease in their accumulation was noted in seeds that severely affected seed quality (Sinha et al. 2000).

In addition, several studies have reported beneficial role of boron in plant growth and metabolism by regulating processes such as auxin and phenol metabolism (Camacho-Cristóbal et al. 2018), formation of flowers and subsequent seed production (Zohaib et al. 2018) and membrane function (González-Fontes et al. 2014).

4.2 Silicon

In plant growth and metabolism several essential macro- and micronutrients play a central role. Many plant scientists, do not consider silicon (Si) as an essential plant nutrient. However, a plethora of evidence has been generated in recent years to suggest a cardinal role of Si in determining plant growth and quality. In addition to being central in governing important biological processes of plants such as transpiration and photosynthesis, Si adapts a plant to grow in adverse conditions of nutrient deficiency, drought, temperature etc. Si supplementation has seen positive effects on plant growth and development in many plants species. This effect was seen more pronounced in plants where plants growing in soils with limited Si concentration were supplemented with optimum Si. In the same study, Si accumulated in a different plant tissue was found to vary between different species, suggesting that the affinity for Si uptake and localization varies between different plant species and tissues, respectively. Plants growing in soils with increased cadmium concentration when supplemented with Si displayed lower ROS species compared to control plants (Hasanuzzaman et al. 2017), suggesting role of Si in antioxidant defence mechanisms. In addition to improving antioxidant defence mechanisms against Cd stress, Si has been established to augment glyoxalase pathways, increase activity of AsA-GSH and production of antioxidant components. Varying dosage of Si supplementation was found to revive Si-deficient plants significantly. In *Zinnia* and *Helianthus* robust stem structures found associated with Si supplementation. The flower size was found increased in *Gerbera* following Si foliar sprays. In all these species, the flower quality increased and flowering time was found substantially reduced with silicon treatments compared to control plants.

Deciphering role of Si in disease resistance and flower size has intrigued a lot of scientists globally. Si supplementation reduces water loss by plants making this research relevant in present times. Si regulates this aspect by regulating development of a waxy layer on plant that significantly reduces rate of transpiration by the plant. Reduction in transpiration rates has proven benefits to plants. Si supplementation was found to regulate functioning of the stomatal valves, thereby affecting stomatal conductance. While growing in greenhouses, the leaves transpired less with increased Si supplementation. While this study implicates role of Si in regulating stomatal conductance, an active role of Si in the process remains to be established with certainty. In addition, Si has also been implicated to alleviate heat stress in plants as it imparts thermal stability to lipids in cell membranes. However, the mechanism remains uncharacterized thus far.

A role of Si has been reported in preventing incidences of powdery mildew disease. Kanto et al. (2009) found that with increase of Si content in leaves, the incidences of powdery milder disease substantially decreased. Similarly, in wheat and barley Si deficiency was found associated with susceptibility to powdery mildew and poor growth (Zeyen et al. 2002). Use of Si foliar sprays was found to prevent powdery mildew disease in grape, muskmelon and cucumber (Bowen et al. 1992).

Datnoff (2005) reports prevention from several disease in turf grass with application of Si foliar sprays. Si supplementation has also been reported to alleviate various chemical stresses such as metal toxicity, nutrient imbalance and salinity. In rice and barley Si supplementation was found to benefit the plant phosphorus deficiency. Beneficial effects of Si include improved structural cell strength, improved absorption of nutrients and reduced salt stress.

One of the first Si sprays to be extensively used is 13 Essentials. It is the first foliar nanoscale (particle size of 1–30 nm) fertilizers to be commercialized in the US market. It boasts an optimum mix of primary nutrients (P and K), secondary nutrients (Ca, Mg and S) and micronutrients (Fe, Cu, Mn, B, Zn, Co and Mo) adsorbed on a nano-silica base. In this foliar spray, Si serves as both a carrier for other nutrients and a nutrient, thereby reducing the possibility of complexing and making the nutrients efficiently available to the plants.

4.3 Selenium

Selenium is an important trace chalcogen metalloid which exists in very low concentration in the earth (Hawrylak-Nowak et al. 2014; Pilon-Smits et al. 2009). Selenium essentiality for the optimal development in higher plants has been well debated (Terry et al. 2000). However, the consistent efforts in this field of research have confirmed the role of selenium in plant's growth (Hartikainen and Xue 1999; Hawrylak-Nowak et al. 2014), reproduction (Cao et al. 2018; Hladun et al. 2013), metabolism (Schiavon and Pilon-Smits 2016; Ning et al. 2013) and in delaying senescence (Rahmat et al. 2017; Pukacka et al. 2011). In addition, it has been established to play a significant role in tolerance against various stresses such as oxidative stress (Mroczek-Zdyrska and Wójcik 2012), biotic stress (Hanson et al. 2004) and abiotic stress (Malerba and Cerana 2018; Nawaz et al. 2015). Table 1 shows some of important studies on the role of selenium in plants.

Table 1 Significant studies highlighting the role of selenium in plants

Sl no	Plants	Effects	References
1	<i>Triticum aestivum</i>	Drought stress	Nawaz et al. (2015)
2	<i>Acer saccharinum</i>	Recalcitrant	Pukacka et al. (2011)
3	<i>Oryza sativa</i>	Biofortification	Boldrin et al. (2013)
4	<i>Cucumis sativus</i>	Salt stress	Hawrylak-Nowak (2009)
5	<i>Brassica rapa</i>	Increases seed production	Lyons et al. (2009)
6	<i>Spirulina platensis</i>	Decreases Cr uptake	Belokobylsky et al. (2004)
7	<i>Brassica juncea</i>	Aphids resistance	Hanson et al. (2004)
8	<i>Lactuca sativa</i>	Antioxidative and growth promoting	Xue et al. (2001)

5 Metalloid Distribution in Plants

Many metalloids are considered an essential micronutrient for higher plants because of assigned important roles in various processes. These metalloids' concentrations in plants are directly related to phyto-availability of these elements in the soil due to natural presence, anthropogenic contamination or foliar application of fertilizers (White 2015; Camacho-Cristóbal et al. 2018). In addition, these beneficial elements are taken in different forms by many transporters (Ding et al. 2008; Archana and Verma 2017; Kumarathilaka et al. 2018). In addition, there are few articles in the literature that have tabulated distribution of various metalloids in various genera and species (Pilon-Smits et al. 2017; White 2015; Camacho-Cristóbal et al. 2018). Table 2 shows the distribution and accumulation of metalloids.

6 Uptake Mechanism and Transporters Involved in Metalloid Uptake in Plants

6.1 Boron Transporter

Boron (B) is an essential metalloid required for the development and growth of the plant. B is an important component of the cell wall that cross-links rhamnogalacturonan-II, a pectic polysaccharide to it, and maintains the integrity of cell wall and growth of the plant (Kato et al. 2009). B deficiency causes a severe impact on the organ expansion including abnormal cell wall, altered cytoskeletal polymerization, defects in the leaf expansion, root elongation, flower and fruit development (Marschner 2012). In plants, B is prevalent in leaves; however, its excess causes the retarded growth, peculiarity of shoots, and chlorosis of leaf tips and margins

Table 2 Accumulation of different metalloids in plant species, parts and regions

Elements	Genera	Regions	Plant parts	References
B	<i>Lycopersicum esculentum</i> , <i>Hordeum vulgare</i> , <i>Brassica napus</i>	Turkey, USA, Asia	Stem, leaves	Pommerrenig et al. (2015), Camacho-Cristóbal et al. (2018)
Si	<i>Oryza sativa</i> , <i>Glycine max</i> , <i>Helianthus annuus</i>	China, Southeast Asia, Africa	Stem, leaves, straw, flag leaf, husk and grains	Ma and Yamaji (2015)
As	<i>Oryza sativa</i> , <i>Pteris vittata</i>	China, Southeast Asia	Stem, leaves, straw, husk, germ, and grains	Kumarathilaka et al. (2018)
Se	<i>Astragalus praelongus</i> , <i>Brassica oleracea</i> , <i>Stanleya pinnata</i> , <i>Lecythis ollaria</i>	USA, Australia, China, Mexico, Europe	Fruits, stem, leaves, Cladodes	Pilon-Smits et al. (2017), Lindblom et al. (2018)

(Reid and Fitzpatrick 2009). Toxicity mediated by B is prevalent throughout the world, including Turkey, South Australia, Mediterranean countries, Chile and California (Miwa and Fujiwara 2010). In plants, B transportation is mainly done from root to shoot through the symplastic and apoplastic movements. Studies using sunflower suggested the passive mode (gradient) of transportation of B (Dannel et al. 2000). Boron is generally present in soil solution as boric acid and is taken up by the plants in the same form. Boron is transported in the plants through two transporters BOR1 and NIP5;1, which are involved in efficient translocation of boron under its deficit. NIP5;1, boron importer, is a member of nodulin-26-like intrinsic protein (NIP) subfamily of the aquaporins (Maurel et al. 2015). High boron concentrations lead to reduction in the expression of level of NIP5;1 root elongation and root hair zone. It is established as an essential transporter. A T-DNA insertion mutant of *nip5;1* was found to have reduced biomass and plant growth under boron-limited conditions (Tanaka et al. 2011, 2016). In maize, TASSEL-LESS1 (TLS1) gene encodes NIP3;1, an aquaporin family member and orthologue of *Arabidopsis* NIP5;1 which is involved in boron transport under boron deficiency (Durbak et al. 2014). In rice, Os NIP3;1 (homolog of AtNIP5;1), is induced during plant growth and development under B-deficient conditions (Hanaoka et al. 2014). In contrast to *nip5;1* which displays decreased root and shoot growth under boron deficiency, *bor1-1* mutant encoding boron transporter 1 shows reduction only in shoot tissue under B deficit. Promoter studies for BOR1 identified it to be expressed chiefly in the root pericycle cells, and BOR1–green fluorescent protein (GFP) fusion protein was localized to the plasma membrane. Further, experiment done on BOR1 mutant yeast complemented with *Arabidopsis* BOR1 led to a threefold reduction of boron in yeast cells implying BOR1 is an exporter of B. It was also the first B transporter to be identified in the biological system (Tanaka et al. 2008). Rice has four copies of Bor1-like gene which is less compared to the *Arabidopsis* which has seven copies of the same gene. Of the four genes, OsBOR1 has the maximum similarity to AtBOR1. OsBOR1 plays an important role in B acquisition by roots and translocation into shoots (Nakagawa et al. 2007).

6.2 Silicon Uptake and Transportation in Plants

Silicon (Si) is the second most copious element after oxygen in soil. Silicon dioxide comprises 50–70% of the soil mass. Abundance of Si in the soil and no visible effects of deficiency led to the consideration that Si is not important for plant growth and yield. Although Si is still not known as essential for plant growth and development, the beneficial effects of this element on the growth, development, yield and disease resistance have been observed in a wide variety of plant species like rice and sugarcane. For example, Si provides resistance against various biotic (Fauteux et al. 2006; Marschner 2012) and abiotic stresses, including drought stress, salt stress, water logging, metal toxicity, nutrient inequity, radiation exposure, freezing and heat (Ma 2004; Coskun et al. 2016), especially for crops like rice and sugarcane.

Plants take up Si as silicic acid $[\text{Si}(\text{OH})_4]$ from the soil. Si content in plants is equal to or greater than the macro-nutrients N, P, and K, which are supplied through fertilizers (Meena et al. 2014). There are two types of Si transporters in plants: (a) channel type transporters and (b) efflux transporters. Low Silicon1 (Lsi1) and Lsi6 belong to the influx- or channel-type transporters of silicic acid. Lsi1 is a member of nodulin-26-like major intrinsic protein III (NIP III) subgroup of aquaporins and acts as a Si-permeable channel. It is localized in different tissues in different plants, for example, rice Lsi1 is localized in the lateral side of root exodermis and endodermis (Ma et al. 2006). Lsi1 in maize and barley is present in the epidermis and cortex (Mitani et al. 2009; Chiba et al. 2009). Si is transported bidirectionally by Lsi1. However, Si taken up into the root cells by *Lsi1* is instantly effluxed out of the cells by another transporter Lsi2 in rice, generating a concentration gradient from the external solution to the root cells; thus, Lsi1 only functions as an influx transporter in rice roots (Mitani et al. 2008; Ma et al. 2006). Maize Si influx transporters (ZmLsi1 and ZmLsi6) are homologues of OsLsi1 and OsLsi6, respectively, but unlike OsLsi1 their expression is not affected by Si availability (Mitani et al. 2009). *OsLsi2* was first identified in rice; further, its homologues were reported in other plant species. Although *OsLsi2* works in conjunction with *OsLsi1*, they do not bear any structural similarity with *OsLsi1* transporters (Ma et al. 2007). In *Arabidopsis*, the *AtLsi2*-like transporters are prevalent compared to the *AtLsi1* (NIPIII), emphasizing dominant role of *OsLsi2*-like transporters. In tomatoes, the NIPIII and *Lsi2*-like transporters are not involved in the Si accumulation (Mitani et al. 2005) that confirms the role of other factors like gene expression, localization, polarity of the transporters, and others in the Si transportation and accumulation.

6.3 Selenium Transporter

Selenium (Se) is an essential trace element for humans and animals. Selenium in soil varies from 0.01 to 2 mg kg⁻¹, and in selenium-rich areas, Se content <1200 mg kg⁻¹ has been reported (Fordyce 2005; Stroud et al. 2010). Elevated Se concentration is toxic to the living organisms since it bears chemical similarity to S that might cause the replacement of S by Se in the proteins (Terry et al. 2000). It also affects the enzymatic activity of peroxidases, which catalyses the oxidation of thiols leading to reactive oxygen species (ROS) production harmful to the plants (Groppa et al. 2007). Se from the soil is acquired in the form of selenate (SeO_4^{2-}), selenite (SeO_3^{2-} ; HSeO_3^- ; H_2SeO_3) or organoselenium compounds, such as selenocysteine (SeCys) and selenomethionine (SeMet) (White and Broadley 2009). Selenate is the major water-soluble form of Se in aerobic soils, while selenite mostly occurs in anaerobic soils such as paddy soils (Pilbeam et al. 2015). Selenate is taken up by the root cells through high-affinity sulphate transporters (HASTs), homologous to the *Arabidopsis thaliana* sulphate transporters (*AtSULTR1;1* and *AtSULTR1;2*) (Gigolashvili and Kopriva 2014). Similarly, enhanced uptake of selenate in S-starved wheat plants validates the positive relation of sulphate transporter with selenate uptake since plants upregulate the expression of sulphate transporter genes in roots

under sulphur starvation (Buchner et al. 2004; Li et al. 2008). Unlike selenate, sulphur starvation did not have significant effect on selenite uptake in major crops like wheat and rice (Li et al. 2008; Zhang et al. 2006). However, in wheat, selenite uptake was found to be enhanced under the phosphate starvation, which expectedly increases the expression of the phosphate transporter genes (Li et al. 2008). In rice, phosphate transporter, OsPT2, mediates selenate uptake (Zhang et al. 2014a), whereas selenite is transported via OsNIP2;1 transporter encoding aquaporin channel (Zhao et al. 2010b). Selenite assimilated through roots is readily converted to organic forms such as selenomethionine (SeMet) and selenomethionine Se-oxide hydrate (SeOMet) (Li et al. 2008), and only slight selenite was transported into xylem. Faulty incorporation of the products such as SeMet or SeCys in proteins distorts structure as well as function of protein and poses toxicity in plants (Fig. 1) (Gupta and Gupta 2016).

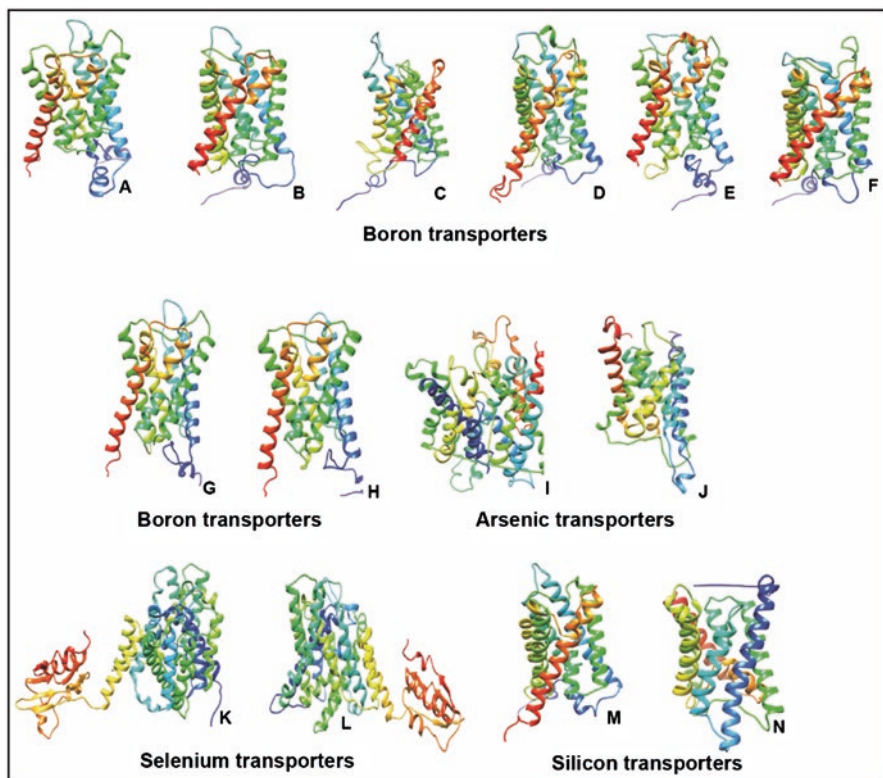


Fig. 1 Model structures of various metalloids transporters: (a) OsNIP3.1, (b) OsNIP3;2, (c) OsPIP2;4, (d) OsPIP2;6, (e) OsPIP2;7, (f) AtNIP3;1, (g) AtNIP5;1, (h) AtNIP7;1, (i) AtBOR4, (j) AtTIP4;1, (k) AtSULTR1;1, (l) OsSULTR1;2, (m) SbLsi1 and (n) OsLsi2 generated using PHYRE2 web portal (<http://www.sbg.bio.ic.ac.uk/~phyre2>) (Kelley et al. 2015). Image coloured by rainbow N → C terminus

7 Co-Transporters Like Arsenate and Citric Acid Transporters

7.1 Arsenate Transporters in Plants

Arsenic (As) is a toxic metalloid with an estimated concentration of 1.5–3 mg kg⁻¹ in soil (Farooq et al. 2016). Several natural processes like the weathering of rocks, volcanic emissions, hot spring releases, mining, smelting and others are the major sources of As pollution. Among the major crops, rice readily takes up As and translocate it to the grains, making it unfit for the population dependent on it (Zhao et al. 2010a). Arsenic exists in the form of several inorganic and organic forms. Arsenate [As(V)] is the major inorganic form in aerobic soils while arsenite [As(III)] predominates in anaerobic soil environment. Organic forms of As include methylated species such as monomethylarsonic acid (MMA) and dimethylarsinic acid (DMA) (Mendoza-Cózatl et al. 2011). As(V) is transported in the plants via phosphate transporters due to the structural similarity with phosphate (Pi). PHOSPHATE TRANSPORTER1 (*Pht1*) proteins are characterized by 12 membrane spanning domains bearing similarity to the yeast Pho84p high-affinity Pi transporter (Rausch and Bucher 2002). Among the phosphate transporter family, *Arabidopsis thaliana* *PHT1;1* and *PHT1;4* are the two high-affinity transporters involved in As uptake. Further, *pht1;1pht1;4* double mutant in *Arabidopsis* was reported to have tolerance against As(V) stress, suggesting major role of these transporters towards As(V) uptake (Shin et al. 2004). Later a study by González et al. (2005) reported the role of *Arabidopsis* mutant defective in phosphate transporter traffic facilitator 1 (*PHF1*) (involved in trafficking of *PHT1;1* from endoplasmic reticulum to plasma membrane) in arsenate metabolism. *Atphf1* mutant was found to have greater tolerance towards arsenate stress compared to the wild type emphasizing importance of *Pht1;1* in arsenate uptake. The mutants of the PHS family like the *AtPht1;1* have slow As uptake, but it accumulates twice compared to the wild type (Catarecha et al. 2007). Another study by DiTusa et al. (2015) reported *PvPHT1;3*, a novel *PHT1* member cloned in the As hyper-accumulating fern *Pteris vittata*, to have comparable and a higher affinity for Pi and As(V), respectively, compared to *Arabidopsis thaliana* *AtPHT1;5*. In rice, *OsPht1;8*, transporter which is expressed in both the root and shoot tissue independent of Pi supply, possesses high affinity for both Pi and As (V). Plants overexpressing *OsPht1;8* in rice show increased As(V) uptake and translocation (Wu et al. 2011). Transcript abundance of *OsPht1;8* is known to be regulated by the transcription factor OsPHR2 (Pi starvation response 2) (Wu et al. 2011). Similarly, high-affinity phosphate transporter, *OsPht1;1*, located in the plasma membrane participates in the As transportation in rice (Kamiya et al. 2013). The regulatory mechanisms governing Pht transporters are still not well defined, but WRKY transcription factors like the WRKY6 and WRKY45 are found involved in the As influx (Castrillo et al. 2013; Wang et al. 2014). WRKY6 is reported to regulate As(V) uptake by repressing expression of the As(V)/Pi transporter *PHT1;1* (Castrillo et al. 2013).

7.2 *Citric Acid Transporters*

Carboxylates like the malate, fumarate and citrate are known to be major constituents of the living system. These metalloids are involved as a precursor or intermediates in the energy, metabolism, biomolecule synthesis, chelators for metallic nutrients and the heavy metals (Ovecka and Takac 2014). Citric acid is a major metalloid that is reported as an iron chelator and is transported by the multidrug and the toxin extrusion (MATE) class of transporter family (Wu et al. 2014). This transporter family is induced during the Fe deficiency.

Citrate transporters like Ferric Reductase Defective 3 (FRD3), OsFRDL1, MtMATE66 and MtMATE69 are prevalent in the leaves, roots and stem that required for the root–shoot translocation of metal ions (Durrett et al. 2007; Yokosho et al. 2009; Pineau et al. 2012). Some transporters like HvAACT1 in barley (Furukawa et al. 2007) and SbMATE in sorghum (Doshi et al. 2017) are well studied. Some of the transporters for the citric acid transportation are FRD3, OsFRDL1 and MATE (multidrug and toxic compound extrusion or multi-antimicrobial extrusion).

FRD3 protein belongs to the multidrug and toxin efflux family that participates in transportation of the chelators like the citrate for efficient distribution of iron throughout the plant (Durrett et al. 2007). Its effluxes citrate into the xylem to form a ferric–citrate complex. The other well-known transporter for the citrate transporter in rice is the OsFRDL1 that shares homology to the HvAACT1 (barley citrate transporter) (Furukawa et al. 2007). This transporter is localized in the pericycle of the cell and transports Fe–citrate complex to the shoot. MATE class of transporters is another well-known citrate transporter which is 400–550 amino acid long comprising 12 transmembrane domains (TMDs). They are involved in the transportation of the secondary metabolite out of the cytosol due to the electrochemical gradient of membrane. They also referred to as a DETOXIFICATION (DTX) protein that participates in the detoxification of the heavy metal contaminants, disease resistance and other biological processes. MATEs are primarily involved in the Al³⁺ detoxification and the Fe uptake by forming complex with the citrate.

7.3 *Transporters Unanimously Transporting Beneficial and Harmful Metalloids: Aquaporins*

Water transporters that were purified forming the red blood cells were first reported by Peter Agre (Agre et al. 1993). This water channel was later characterized using the *Xenopus* oocyte and named aquaporins1 (AQP-1) that belongs to the major intrinsic protein (MIP) family (Deshmukh et al. 2013). The MIP family comprises aquaporin (water and ion transportation), the glycerol facilitators (glycerol transportation) and the aqua glyceroproteins (water and small uncharged molecules like polyols, urea and arsenite). This family comprises the six transmembrane domains

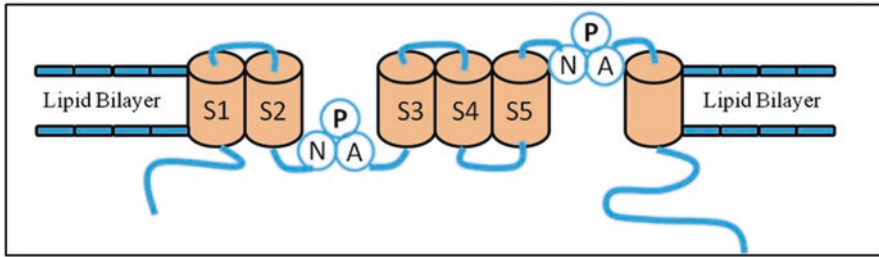


Fig. 2 A typical structure of aquaporin channel in plants

with five loops, and an N-terminal and C-terminal domain (Frick et al. 2014). At the centre, it has an NPA (Asn–Pro–Ala) motif that provides the substrate selectivity (Fig. 2) (Kitchen and Conner 2015).

7.3.1 Aquaporins in Plants

The tonoplast protein γ -TIP (AtTIP1;1) of *Arabidopsis* is a first characterized aquaporin (Rivera-Serrano et al. 2012). The aquaporin transporters are involved in different physiological processes like the cell elongation, seed germination and osmoregulation. A total of 35 MIPs are known in *Arabidopsis* (Deshmukh et al. 2013), 36 in maize (Bansal and Sankaramakrishnan 2007) and 33 in rice (Sakurai et al. 2005) compared to the mammals (Borgnia et al. 1999), *Escherichia coli* (Agre and Kozono 2003) and *Saccharomyces cerevisiae* (Pettersson et al. 2012). The higher number of aquaporins is due to continuous water absorption, flux and evaporation during growth and development (Li et al. 2014).

7.3.2 Aquaporin Mode of Activity

Aquaporin has Ar/R (aromatic–arginine) pore region that is located near to the NPA–NPA region and provides selectivity to the transporter (Deshmukh et al. 2013). In NIPs, the Ar/R provides an additional advantage by allowing neutral metalloids, undissociated acids and small solutes like glycerol across the plasma membrane.

8 Transgenic Plants with Improved Uptake of Beneficial Metalloids

From the last two decades, the researchers have expedited the field of transgenic biotechnology several folds mainly with advances in high-throughput transformation protocols, donor genes isolation from diverse organisms and available

databases (Mitani et al. 2011; Deshmukh et al. 2015; Song et al. 2017). As a result, the scientists have pushed their research prospects in improving the photosynthetic capacity, yield, nutrition content, aroma, biotic stress tolerance, heavy metal toxicity and metalloids uptake (Helliwell et al. 2013; Quilis et al. 2014; Kudo et al. 2017; Bardor et al. 2018). This is also evident from the fact that the term ‘transgenic plants’ fetched around 517,000 publications in the Google scholar (<https://scholar.google.co.in/>). It is very challenging to include all the transgenic plants in this book chapter; therefore, we will only list about the main transgenic plants with improved uptake of beneficial metalloids (Wang et al. 2017, 2018; Sun et al. 2017; Song et al. 2017; Mitani et al. 2011; Pérez-Castro et al. 2012; Tanaka et al. 2013; Chen et al. 2017).

8.1 Enhancement of Boron Uptake

Besides being rare element, B is considered as an essential element for normal growth, development, metabolism, signalling and reproduction in plants (Camacho-Cristóbal et al. 2018). Earlier it was a notion that the plant cells maintain the levels of boron at optimum concentration through unregulated simple diffusion (Dannel et al. 2000). However, Takano and co-workers (2002, 2008) discovered the involvement of specific transporter proteins in boron trafficking across the roots cell membrane and xylem loading. Their finding was also supported by the work of Miwa et al. (2006) and other groups (Uraguchi and Fujiwara 2011; Marschner 2012). Therefore, the understanding is necessary to manipulate and develop plants that are resistant to B deficiency and toxicity. Due to this, the researchers have aimed their research prospects in understanding the (1) molecular aspects of the transporters of these metalloids; (2) role in uptake, distribution and utilization; (3) effects of deficiency or toxicity of metalloids; and (4) development of plants with increased metalloids use efficiency (Camacho-Cristóbal et al. 2018). As a result, the scientists have made multiple transgenic plants over the last decades (Pang et al. 2010; Pérez-Castro et al. 2012; Tanaka et al. 2013; Wang et al. 2017).

Miwa et al. (2006) developed the *Arabidopsis* transgenic lines by overexpressing *AtBor1* and reported the enhanced tolerance to B-deficient conditions and increase in the seed content. Kato and group (2009) overexpressed the *AtNIP5;1* in *A. thaliana* plants and observed an increase in the tolerance to B-deficient conditions. They speculated the enhanced tolerance was probably due to enhanced B initial uptake.

Pang et al. (2010) overexpressed the *AtTIP5;1* in *Arabidopsis* and found a significant increase in tolerance under high boron conditions. Tanaka et al. (2013) examined the OsBOR4 function in relation to the accumulation of boron in the leaves and flowers by using the knockout mutant lines in rice. Their results established that OsBOR4 is cardinal to the reproductive process in rice. Similarly, the overexpression of *AtBOR1* in *Solanum lycopersicum* showed a better survival under the B-deficient conditions (Uraguchi et al. 2014). Takada and group developed *AtBOR2* overexpression lines in

Arabidopsis and found the enhancement in root growth and seed setting under B-deficient conditions (Takada et al. 2014). Additionally, the *AtBOR1* orthologous genes have been overexpressed in plants, including citrus, grape, maize and rice (Nakagawa et al. 2007; Pérez-Castro et al. 2012; Cañon et al. 2013; Chatterjee et al. 2014) growing under B-deficient conditions.

Kumar et al. (2014) characterized the role of *OsPIP2;7* and *OsPIP2;4* genes in B permeability. They found that the high B conditions elevated the *OsPIP2;7* and *OsPIP2;4* expressions in rice roots using transcriptome analysis. Furthermore, they heterologously overexpressed *OsPIP2;7* and *OsPIP2;4* in the *A. thaliana*. The overexpression lines displayed a significant enhancement in higher biomass, root length and shoot length. Furthermore, there was an increase in B accumulation in transgenic plants in comparison to the control plants. Hanaoka et al. (2014) characterized the *OsNIP3;1* in rice (*Oryza sativa*). They expressed the *OsNIP3;1* gene in yeast cells and found the enhancement in the uptake of boric acid compared to control cells. They even heterologously expressed GFP-tagged *OsNIP3;1* in the tobacco plant and reported the *OsNIP3;1* localized to the plasma membrane of exodermal and pericycle cells. Furthermore, they revealed the *OsNIP3;1* transcript accumulation increased up to fivefold in roots under low B conditions only. Even, using RNA-interference (RNAi) technology, the effect of *OsNIP3;1* knockout was seen on growth under different B supply. In another instance, Liu and group characterized a dwarf and tiller-enhancing 1 (*dte1*) mutant of rice, which exhibited many defects such as impaired pollen fertility, retarded growth and more numbers of tillers under low B conditions. Using RNA-interference, transgenic complementation and map-based cloning, they revealed the *DTE1* gene encodes an *AtNIP5;1* orthologue. In addition, they found the subcellular localization using β -glucuronidase (GUS) staining and studied the *DTE1* transcript accumulation profile in vegetative organs under B starvation. The RNAi mutant lines showed a steep decline in the total B content under B-deficient conditions.

Similarly, Wakuta et al. (2015) studied the polar localization and evolutionary divergence in borate exporter family. Additionally, they generated both *AtBOR1* overexpression and RNAi mutant lines to study boron-dependent vacuolar sorting. In another study, Mosa et al. (2016) provided the experimental evidence about the bidirectional transport of boron by *OsPIP1;3* and *OsPIP2;6* in rice. Heterologous overexpression of *OsPIP2;6* and *OsPIP1;3* in *A. thaliana* led to enhancement of tolerance to B toxicity. Interestingly, the *10B* was effluxed from the roots in the transgenic plants. More recently, Wang and co-workers (2017) studied the role of clathrin-mediated endocytosis in *NIP5;1* polar localization of epidermal and endodermal cells in the roots. Additionally, they found the role of arrangement is mediated by the phosphorylation of Thr residues of the N-terminal region. Lv et al. (2017) reported a *shb1* (sensitive to high level of boron 1) mutant which exhibited hypersensitivity under high boron conditions. They found that *SHB1* gene upregulates in roots under excessive boron treatments. Additionally, it upregulates the transcription of the *BOR4* gene and alters the boron uptake in root cells. More recently, Porcel et al. (2018) screened complementary DNA (cDNA) library of *Beta vulgaris* and identified a *BvCOLD1* gene which codes for a protein with a role in the

transport of several molecules, including boron. The heterologous overexpression of *BvCOL1* in *A. thaliana* led to enhancement in tolerance against many abiotic stresses as well as boron uptake.

8.2 Silicon Uptake and Transgenic Plants: A Short Story

In the earth's crust, silicon is the second most abundant element; however, it is considered important for plant defence. In the literature, the articles about the transgenic plants with higher uptake of silicon are very less. For the first time, Ma and group (2006) described the low silicon rice 1 (*Lsi1*) gene in the *O. sativa* cultivar Oochikara, which plays a role in silicon accumulation. They studied the cellular and subcellular localization; in addition, they reported the *Lsi1* RNAi plants that showed a decline in silicon uptake. Similarly, Chiba et al. (2009) described the cellular and subcellular localization of *Lsi1* gene in *Hordeum vulgare*. They heterologously expressed the *Lsi1* gene in mutant rice with defects in Si uptake. Surprisingly, the *HvLsi1* expression enhanced the Si uptake and radial transport in rice. In another instance, Montpetit and co-workers (2012) functionally characterized *Lsi1* gene in wheat. In addition, they heterologously expressed *TaLsi1* and *OsLsi1* orthologues in *A. thaliana*. The heterologous expression significantly increased the uptake by fivefold in overexpression *Lsi1* lines in comparison to the wild-type control plants. Similarly, Dallagnol et al. (2013) evaluated the effect of soluble silicon on the wild-type and mutant rice plants with defects in the *Lsi1* transporter. In addition, they evaluated the effect of *Bipolaris oryzae* on biomass accumulation, photosynthesis and soluble sugar levels. In another study, Mitani and co-workers (2011) identified a Si influx transporter in *Cucurbita moschata* cultivars Super-unryu and Shintosa. They isolated this transporter and expressed in a rice mutant with a defect in Si uptake. The transgenic lines showed the heterologous expression led to the influx of Si. In addition, the amino acid change of proline to a leucine at the position 242 by site-directed mutagenesis leads to Si transport activity loss. In another study, Fang and workers (2011) evaluated the role of the *Lsi1* transporter in the defence against Ultraviolet B (UV-B) stress in rice. In order to elucidate, they generated both overexpression and knock-out *Lsi1* lines and subjected to UV-B stress. They found a correlation between the *Lsi1* transcript levels with Si uptake in roots. In addition, they reported the *Lsi1* upregulated expression of genes related to resistance and photosynthesis, including phenylalanine ammonia-lyase using suppression subtractive hybridization. In another study, Deshmukh et al. (2015) characterized the NIP-III aquaporins which play a role in Si permeability. They performed the comparative analysis of more than 100 aquaporins in many species and predicted about 30 Si transporters with a GSGR filter and significant asparagine–proline–alanine (NPA) domain. In addition, they assessed the effect of 108 amino acids spacing on Si permeability on poplar and tomato mutants. Recently, Sun et al. (2017) studied the cellular localization and functionally characterized the *CsLsi1* gene in *Cucumis sativus* cultivar Mch-4. The *CsLsi1* gene heterologous expression in a mutant rice significantly enhanced the silicon uptake.

8.3 *Transgenic Plants with Enhanced Selenium Uptake*

Compared to the other metalloids, the publications for the transgenic plants with higher uptake are very few (Ellis et al. 2004; LeDuc et al. 2004; Zhao et al. 2010b; Zhang et al. 2014b; Song et al. 2017). The trial of adenosine triphosphate (ATP) sulphurylase (APS) transgenic lines in a greenhouse pot experiment displayed accumulation of Se more than threefold levels compared to wild-type *Brassica juncea* (Huysen et al. 2004). Ellis et al. (2004) isolated the SeCys methyltransferase (SMT) gene from the donor *Astragalus bisulcatus*, and the heterologous overexpression in *A. thaliana* led to a slight increase in the overall uptake of selenate. Similarly, LeDuc and colleagues overexpressed the SMT gene in the plant *B. juncea* and found the changes in the profile of Se volatilization, uptake, transport and accumulation (LeDuc et al. 2004). Later, the same group developed ATP sulphurylase (APS), SMT transgenic and double transgenic APSxSMT lines and compared the accumulation efficiency of all transgenics to the control plants (LeDuc et al. 2006). Sors et al. (2005) overexpressed the Adenosine 50-phosphosulphate reductase (PaAPR) in *A. thaliana*. The transgenic lines showed an increase in selenite uptake in comparison to the control plants. Banuelos and co-workers (2005, 2007) heterologously expressed the AtATPS1 and SMT in the plant *B. juncea* and observed an increase in selenate uptake. Additionally, they performed the field trials of these transgenic Indian mustard lines and reported no effect on the Se tolerance in the rhizosphere. El Kassis and group (2007) characterized the SULTR1;2 and SULTR1 transporters from *A. thaliana* mutant and confirmed their role in selenite uptake using a gain of function approach. Additionally, they confirmed the SULTR1;2 play a predominant role in selenate uptake. In another study, Zhang and co-workers (2014a) confirmed that OsPT2 is a negative regulator of selenite (HSeO₃) uptake using OsPT2 overexpression and RNAi plants. In another instance, Zhao and co-workers (2010b) evaluated the role of OsNIP2;1 in the uptake of H₂SeO₃ in rice plant using mutant analysis and expression studies. Their work was also supported by the Pommerrenig and group (2015).

Recently, Song et al. (2017) reported the role of OsPT8 in Se uptake in tobacco. The OsPT8 overexpression in the tobacco plant led to a significant increase in the biomass, total P concentration and Se accumulation in comparison to the control plants. More recently, Wang et al. (2018) studied the differences in transcriptome profiles of shoot and root from *Stanleya pinnata* and *S. elata* when grown with or without selenite supply. They reported that genes related to selenate cycle, defence-related, oxidative stress resistance and antioxidant activity were found highly upregulated in the *S. pinnata* compared to the non-accumulator species. They reported the Se hyper-accumulation as well as hyper-tolerance were due to upregulation of SA, ethylene and JA pathway genes. They highlighted that these upregulated genes will be the targets of biofortification mediated by genetic engineering in the future publications.

8.4 Manipulating the Arsenic (As)

In the environment, arsenic is present as a well-known metalloid which exists in two variable forms, arsenite (As(III)) or arsenate (As(V)). In the recent past, the biotechnological approaches have been used to identify the genes and develop transgenic plants to increase the As uptake (Isayenkov and Maathuis 2008; Remy et al. 2012; LeBlanc et al. 2013; Xu et al. 2015; Chen et al. 2017).

Dhankher et al. (2002) pyramided two bacterial genes, γ -glutamylcysteine synthetase and As(V) reductase, in *A. thaliana* and found enhancement in the accumulation of As in shoots as compared to the control plants. Navaza et al. (2006) overexpressed glutathione synthetase and gamma-glutamyl cysteine synthetase in *Brassica juncea* and observed higher As accumulation and uptake. In a series of publications, Ma et al. (2007, 2006) studied the cellular localization and role of low silicon rice family members (Lsi1 and Lsi2) in As(III) influx and efflux. They knock out the expression of both transporters and studied the effect on As uptake, trafficking and concentrations in the grain and straw. Grispen et al. (2009) heterologously expressed the *Arabidopsis* metallothionein gene in the tobacco and reported the significant change in As accumulation and uptake. Isayenkov and Maathuis (2008) confirmed the role of *AtNIP7;1* in arsenite uptake using overexpression and RNAi. Wu et al. (2011) overexpressed two genes Phosphate transporter (*Pht1;8*) and Phosphate Starvation Response 2 (*PHR2*) in the susceptible cultivar of *O. sativa* and increase in uptake of As(V) and phosphate. The heterologous co-expression of many members of OsPIP family in *A. thaliana* led to enhancement in the plant's tolerance towards *H2AsO3* rather than the enhancement in the As uptake as well as higher biomass accumulation (Mosa et al. 2012). In another instance, the heterologous expression of phytochelatin synthase gene from *Ceratophyllum demersum* in plants such as *Arabidopsis* and tobacco (Shukla et al. 2012, 2013) led to significant enhancement in As uptake and accumulation. However, there was no effect on the plant growth. LeBlanc et al. (2013) overexpressed the *AtPht1;7* gene in *A. thaliana* and observed the significant accumulation of As(V) in transgenic lines.

In another case, it was reported that WRKY45 and WRKY6 regulate the *AtPht1;1* expression of and, hence, modulate As(V) uptake from the soil (Castrillo et al. 2013; Wang et al. 2014). Xu et al. (2015) identified the NIP subfamily to be involved in arsenite uptake. Furthermore, they found *AtNIP3;1* play a role in the arsenic uptake as well as root-to-shoot distribution under different arsenite conditions using reverse genetic strategies. The single *nip3;1* mutant accumulated less arsenic in shoots in comparison to the control plants, whereas the double mutant displayed improved growth in shoots and roots under arsenic stress conditions. They also found the *NIP3;1* gene was expressed exclusively in roots using GUS analysis. Recently, He et al. (2016) characterized a *PvTIP4;1* gene from *Pteris vittata*, which mediates the uptake of As(III) using functional complement cDNA library. Further, they analysed the effect of arsenic accumulation in *A. thaliana*; subcellular localization and the tissue expression profile of *PvTIP4;1*. The transgenic lines showed an increase in

arsenic uptake and accumulation. In another study, Wang et al. (2016) knocked out the *OsPht1;8* gene in rice in order to evaluate the effect on the uptake; contrastingly, they found that As(V) uptake significantly decreased by about 55% in transgenic lines in comparison to the control. Shi et al. (2016) identified the differential expression of *OshAC1;2* and *OshAC1;1* genes in different cells of rice roots under different arsenate treatments. The knockout mutant of both genes displayed a decrease in arsenate reduction and increase in As accumulation in the mutant plants. In the latest study, Chen et al. (2017) reported that *OsNIP3;2* plays a significant role in arsenite uptake in rice lateral roots using mutant analysis and overexpression studies. More recently, Wang et al. (2018) investigated the effects of arsenate reductase, γ -glutamylcysteine synthetase and phosphate effluxer knockout on As tolerance and uptake in *A. thaliana* plants. In addition, their group overexpressed *PvACR3* from the plant *Pteris vittata*. They observed a slight change in As uptake as well as shoot-to-root translocation. All knockout mutants showed higher root-to-shoot translocation of arsenic.

9 Challenges to Improve Solute Specificity

These metalloids are elements with chemical properties between metals and non-metals. They comprise many physiologically important elements with roles in growth, development, reproduction, flowering, stress tolerance, desiccation and ultimately yield. In addition, some are toxic to plants such as arsenic, germanium and antimony as their exposure seriously downgrades the plant's metabolism. However, most of metalloids are considered beneficial for plants, and their uptake, translocation and homeostasis are mediated by various membrane transporters. The large data about these various types of transporters have already been gathered majorly by application of techniques such as the gain of function or loss of function approaches, GUS assays, functional complementation assays and promoter analysis. However, there are still many questions associated with the metalloid transport and transporters which need to be addressed.

In the future, many questions associated with metalloid transport in plants will be addressed, including (1) how metalloid-permeable transporters are regulated on metalloid exposure? (2) how do the various plant species orchestrate the transport of a given metalloid? (3) which motif of transporters determines the metalloid selectivity? (4) at which point in the evolution time scale, the nature abled the transporters to channel two types of metalloids? (5) how do the uncharged forms of metalloids are transported *in planta*? and (6) what are the potential transporters of rare elements such as Po, Te and At? In addition, the researchers will generate plants, especially major crops with higher uptake as well as higher tolerance using both breeding and transgenic approaches.

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