



## Review

## Potential targets to reduce beryllium toxicity in plants: A review

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## ABSTRACT

Industrialization and inevitable mining has resulted in the release of some metals in environments, which have numerous industrial roles on one hand and also showed environmental toxicity on other hand. Beryllium is one of them, it has been used in number of industries however its excess use or inappropriate disposal of beryllium resulted in high beryllium accumulation in soil and ground water. This subsequently is affecting our environment and more potentially arable crop production. Beryllium has been extensively studied in humans and reported as toxic metal. In plants, only few studies have been documented toxic effects of beryllium in plants. Moreover, plant products (fruits, grains or other plant parts) could be major source of beryllium toxicity in our food chain therefore it is more imperative to understand how plant can be developed more tolerant to beryllium toxicity. In this short mini-review article, we primarily highlighted and speculated different beryllium uptake, translocation and beryllium storage mechanism in plants. This article provides considerable information for people who are working in identifying and developing heavy metal hyper accumulators plants.

## 1. Introduction

In our natural environment, heavy metals are deposited in rocks or mines. However global modernization in industry concentrated their concentrations in soil by different processes (Shahzad et al., 2016, 2017; Anjum et al., 2016). Beryllium belongs to Group IIA of periodic table and is very important from industry point of view. Worldwide, it is present around 2.8–5 mg kg<sup>-1</sup> of earth crust (Armiento et al., 2013). Across different countries worldwide, USA produces almost 88% of total beryllium production followed by China (7.4%) and Mozambique (2.2%) (<http://www.statista.com/statistics/264925/world-beryllium-production>). Beryllium has been used from last two decades extensively in medical and defense industry (Shah et al., 2016). World resources relating to beryllium have been estimated to be more than 80,000 tons. About 65% of these resources are in nonpegmatite deposits in the United States; the Spor Mountain and Gold Hill areas in Utah and the Seward Peninsula area in Alaska account for most of the total (U.S. Mineral commodity 2016). Beryllium is very important metal from industrial point view (Fig. 1), as its uses include nuclear weapons and reactors, aircraft and space vehicle structures, instruments, x-ray machines, and mirrors and other industries. All these uses, although contribute in global development and modern industrialization however they are also resulting in releasing beryllium in our ecosystem. There are other sources through which beryllium is being entered in our

environment (Fig. 1), such as smelting and mining of ores results in the discharge of industrial effluents, which contaminate soil and water streams (Shah et al., 2016). Atmospheric emission of beryllium as a result of mining also acts as potential source of beryllium toxicification. Beryllium addition in atmosphere due to coal burning has been reported from 1.8 mg kg<sup>-1</sup> to 15 mg kg<sup>-1</sup> (Lovblad, 1977). Fuel oil can also add up to 100 µg Be L<sup>-1</sup> (Drury et al. 1978). Beryllium is reported to be carcinogenic when inhaled or eaten by beryllium contaminated food (Beyersmann and Hartwig 2008; Cataldo et al., 1987).

Beryllium contamination worldwide is increasing and imposing serious threats to environment and humans (Shah et al., 2016). General sources of beryllium toxicity in humans are food, which were grown and harvested from beryllium contaminated soil or beryllium polluted water (Lovblad, 1977). In water beryllium settles on the bottom with sediments, while insoluble beryllium compounds can remain suspended in ocean water for a few hundred years prior to settle down (Rasheed et al., 2012). Different reports showed different beryllium concentrations in ground water and soil around the world (Fig. 2), suggesting water as one of key sources of beryllium contamination or transfer of beryllium to food (WHO, 2009).

Beryllium concentration varies among different food items, for instance, in kidney beans 2.2 Be mg kg<sup>-1</sup> is reported, in crisp bread 0.112 mg Be kg<sup>-1</sup> is reported, in garden peas and parsley, reported Be concentration is 0.109 and 0.077 mg Be kg<sup>-1</sup> respectively (ATSDR,

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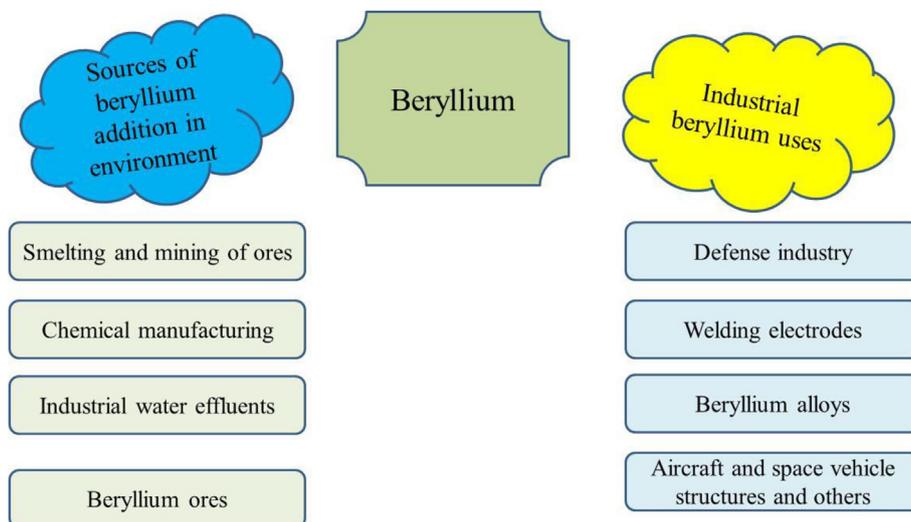


Fig. 1. Sources of beryllium addition in our environment (Left) and industrial uses of beryllium (right).

Country	Different bodies	Beryllium concentration	Reference
Jordan	Ground water	0.006 mg/L	Batayneh, 2012
Mexico	Ground water	0.035 mg/L	Gutierrez et al. 2008
Russia	Ground water	0.009 mg/L	Momot and Synzynys, 2005
Germany	Ground water	$8 \times 10^{-6}$ mg/L	WHO, 2009
Thailand	Surface soil	1.43 mg/kg	Asami and Kubota, 1995
Yugoslavia	Surface soil	1.17 mg/kg	Asami and Kubota, 1995
Japan	Surface soil	3.52 mg/kg	Asami and Fukazawa, 1985
Brazil	Surface soil	0.58 mg/kg	Shacklette and Boerngen, 1984
Worldwide	Surface soil	60 mg/kg	Drury et al. 1978

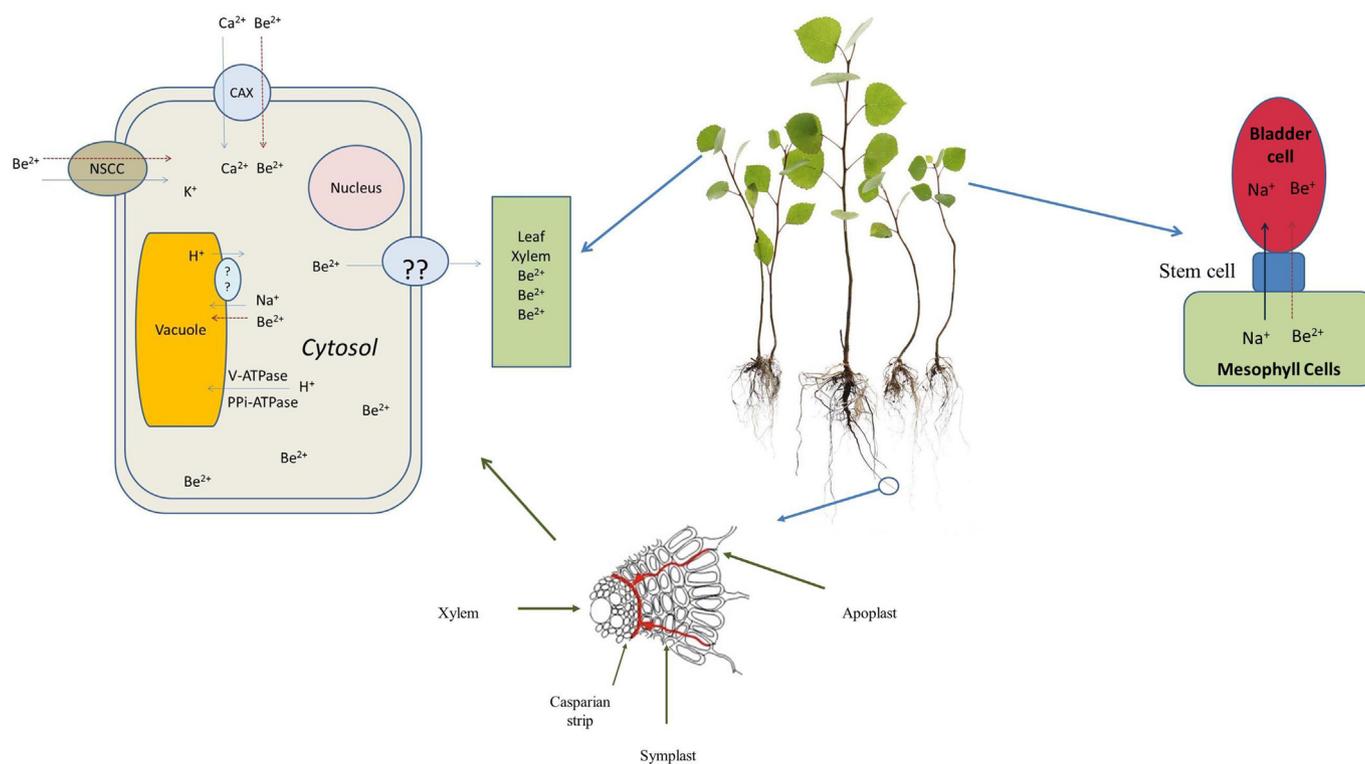
Fig. 2. Beryllium concentration in ground water and surface soil around the world.

2002). Likewise the average concentration of beryllium in fruit and fruit juices was  $13.0 \mu\text{g/l}$  (range from < the detection limit to  $74.9 \mu\text{g/l}$ ) (ATSDR, 2002). These values are clearly indicating that agricultural products are being contaminated with beryllium and thus being transferred to other members of food chain. It is hard to reduce beryllium use in industry due to its extraordinary physical and chemical properties and also due to growing population and increasing demand of beryllium products, but policies relating to the limited use of beryllium or safe disposal of beryllium can save environment and food from being intoxicated. Nonetheless still there are chances of beryllium contamination in environment. Therefore it is imperative to study beryllium toxicity in plants, and we can manage such situation by (1) improving beryllium tolerance in plants so they can uptake less beryllium or restore them in storage organ, which would be not useful as food or (2) adopting different remediation strategies to rehabilitate beryllium contaminated soils. In following section, an overview of beryllium induced toxic effects in plants has been discussed (for more detailed information, see Shah et al., 2016). Moreover beryllium uptake, translocation and accumulation have been discussed and proposed different models to improve beryllium tolerance in plants.

## 2. Plant responses to beryllium toxicity

Optimum plant growth depends on numerous factors such as soil fertility, genetic or environmental conditions. Moreover different elements are important for plant growth however their essentiality depends on their role in plant growth and development and their concentration in growth medium. Some elements/metal ions (e.g. Ni) are beneficial in micro molar concentration however an increase in their concentration from optimum level, retards plant growth and yield (Shahzad et al., 2018). Biological essentiality of beryllium has not been identified in plant yet, however few old studies reported different negative effects of beryllium on plant growth (see Shah et al., 2016). Most important stage in the lifetime of plant is seed germination and stand establishment of seedlings and under stress conditions this stage gets disrupted significantly (Hussain et al., 2018). Beryllium has been reported as toxic element and reduces plant growth by reducing seed germination, root length and dry weight (Kaplan et al., 1990). Similarly, beryllium also reduced the germination of oat and potato tubers, thus reduced overall yield of these crops (Bohn and Seekamp, 1979). After seed germination, root proliferation and root length are most vulnerable to stress induced detrimental effects. In squash, beryllium reduced root length by 4–46% (Hopkins, 1952).

Most importantly, beryllium disturbs energy production, which is



**Fig. 3.** Putative model of beryllium uptake and transport from root to shoot and beryllium sequestration in vacuole and salt bladder cells. Beryllium may enter in root cells via apoplast or symplast. Through apoplast pathway, beryllium may enter into apoplast and transport from one cell to another via cell wall continuum, however it may be stopped by casparian strip. Following this, beryllium has to enter into xylem through symplast. During symplast pathway, different cation transporters (NSCC, CAX) located in plasma membranes may assist in up-taking beryllium in cytosol. It is unknown what kind of transporter is involved in transporting beryllium into xylem. As stress adaptive strategy, plants may either accumulate excess beryllium in vacuoles (left side) or stored in bladder cell (right side) mediated by different transporters. This is proposed model, and it has to be validated yet.

required to carry out several metabolic processes in plants. Beryllium primarily inhibits the activity of phosphoglucomutase and limits the conversion of glucose-1-phosphate to glucose-6-phosphate (Shah et al., 2016). Magnesium is required for the activation of phosphoglucomutase and beryllium can limit such activity by replacing magnesium (Sutherland et al., 1949; Shah et al., 2016). Studies also showed that cysteine also acts as an activator of phosphoglucomutase (Milstein and Sanger, 1961; Aldridge and Thomas, 1966). One possible reason behind beryllium induced inhibition in the activity of phosphoglucomutase might be because of that beryllium may displace magnesium or cysteine, and ultimately reduces phosphoglucomutase activity in plants.

Beryllium can also reduce plant growth by reducing the uptake of other essential micro-nutrients. Several studies showed that beryllium replaces magnesium and causes symptoms similar to magnesium deficiency (Hoagland, 1952a,b; Naidu et al., 1979) and this might be because beryllium may act on same metabolic site where magnesium acts (Shah et al., 2016). However exact mechanism is still unknown. Moreover beryllium and magnesium exhibit similar physical chemical properties and therefore, it is hard to conclude that reduction in growth is due to beryllium toxicity or beryllium induced deficiency of other nutrients. To conclude, beryllium does reduce plant growth however exact mechanism is not known due to the limited number of studies. Therefore it is imperative to study beryllium toxicity in plants and for that it is more important to understand how plant uptake beryllium under high beryllium stress levels.

### 3. Beryllium uptake and transport in plants

Beryllium is widely distributed in environment, so it can be easily up taken by roots. Be accumulation in plant depends on several factors such as Be contents in soil, plant ability to accumulate and co-existence of ions in soil with similar physio-chemical properties and Be transport system.

Availability of beryllium in soil considerably influences beryllium uptake and depends on soil type and clay contents in soil and ionic form of beryllium. More beryllium is available in bentonite soil or other soils with more clay contents as compared with kaolinite soil, which showed less strong bound with beryllium (Romney and Childress 1965). Moreover, high beryllium concentrations were noted in plants grown in Blanton soil and liming of beryllium polluted soils resulted in less beryllium uptake and accumulation in different plant tissues (Sajwan et al., 1996). According to Griffiths et al. (1977), clay contents can absorb between 2 and 5 mg beryllium  $\text{kg}^{-1}$ , while sandstones and limestones contain less than 1 mg  $\text{kg}^{-1}$  (Griffiths et al., 1977). It can be suggested that clay minerals concentrate beryllium through isomorphous substitution in which structural cations present in the tetrahedral and octahedral sheets in clay minerals may be substituted by cations with a similar charge (Shah et al., 2016).

Soil pH and ionic form of beryllium also influences beryllium availability and uptake. In most of soil, beryllium exists as oxidized compound while in calcareous soil it occurs as beryllium carbonates and beryllium bicarbonates (Shah et al., 2016). Nonetheless, it may also present as chlorides or sulfates form and can reduce plant growth (Shah

et al., 2016). Soil with low pH increases the solubility of heavier metals (e.g.) nickel, iron, copper and beryllium in plants are significantly and directly correlated with these metal ions, thus increases beryllium uptake by plants. For instance in acidic soil (low pH soils), beryllium is more toxic to mustard plant as compared with calcareous soils (Williams and Le Riche, 1968). One possible reason behind that liming may ameliorate beryllium induced toxicity in plants or soil with high pH may neutralize beryllium in soil. Similar results were noted by Kaplan et al. (1990) and Hoagland (1952a) who showed that beryllium was more toxic under low pH as compared with high pH. This may also be because in acidic soils, due to reduced negative surface charge, there is less availability of binding sites for cations therefore high solubility of beryllium may result in higher beryllium uptake in different plant tissues (Shah et al., 2016).

Another factor, which also influence beryllium uptake is coexistence of similar ions in growth medium. Beryllium also has similar physical properties with Ca and Mg, and can interact with these elements (Shah et al., 2016). For instance, beryllium toxicity was reduced by application of liming, which showed that Ca can ameliorate beryllium toxicity (Sajwan et al., 1996). Not enough work has been conducted relating to beryllium toxicity in plants, few old testaments are available and it is still unknown that what mechanisms control beryllium uptake mechanism, beryllium translocation mechanism, beryllium sequestration mechanism and beryllium detoxification mechanism in plants. In this section, plausible models have been suggested based on available literature to further highlight the gaps relating to beryllium toxicity and beryllium tolerance in plants.

#### 4. Mechanism of beryllium mobility in plants

Concerning the beryllium uptake and transport, two hypotheses (Fig. 3) can be proposed based on similar properties of beryllium with Ca; (1) beryllium uptake via symplast movement via passive transport using cation transporters and (2) beryllium may enter xylem via apoplast of cells.

#### 5. Beryllium mobility via symplast

In symplast pathway, solutes (e.g. beryllium) enter root endodermis and then move from cell to cell via plasmodesmata. However after entering into apoplast, plant plasma membranes (PM) in roots act as a major and very first barrier to solutes uptake and transport in symplast. Under heavy metal stresses, different heavy metal ions interact with different compartments of PM and induce lipid peroxidation, which consequently results in the loss of PM integrity, leading to serious ion imbalances in the cytoplasm (Devi and Prasad, 1999; Liptáková et al., 2013; Shahzad et al., 2018). Electrophysiological studies showed that upon exposure to heavy metal ions, there are strong changes in membrane potential and PM can be then depolarized. Depolarization in PM further restricts uptake of essential nutrients (such as  $K^+$  or  $Ca^{2+}$ ), and this could be an important parameter while studying beryllium stress tolerance.

In root-soil interface, beryllium uptake from soil in root epidermal cells may occur via plasma membrane via passive transport. Several transporters facilitate movement of ions across PM. Under beryllium stress, few putative transporters such as calcium-proton exchanger (CAX) or non-selective cation channels (NSCC) may play important role in Be uptake and transport (Fig. 3). These transporters have been well studied for Ca homeostasis under different stress conditions (Demidchik et al., 2002; Gierth et al., 2005; Apse and Blumwald, 2007; Shi and Chan, 2014). Beryllium can enter first in root cells via CAX and NSCC transporters and accumulate in cytosol. Then following accumulation in cytosol, beryllium may enter into xylem via unknown transporter by replacing Ca and then may transport to leaves (Fig. 3).

#### 6. Beryllium mobility via apoplast

Beryllium may also transport from one cell to another via cell wall continuum (Fig. 3). Beryllium may enter into apoplast and start moving from one cell to another cell however its transportation across cells would be ultimately stopped by Casparian strip and then beryllium has to enter into cell via symplast. Therefore it is more important to focus on symplast transportation of beryllium as compared with apoplast. A speculation can also be made that under high beryllium toxicity, that beryllium may be transported to xylem via apoplast due to (1) increased transpiration pull or (2) impaired casparian strip. However it has never been validated yet, therefore it should be considered in future studies. Apoplast could be a potential target to limit beryllium entry in cell symplast, as restricting the entry of beryllium in cell via retaining in apoplast could be an important mechanism for improving beryllium stress tolerance in plants. Cell wall plays an important role in heavy metal ion detoxification or accumulation, thus reduces the entry of toxic metal in cells (Weis and Weis, 2004). Different studies showed positive role of the cell wall in heavy metal detoxification under different heavy metal stresses (Hossain et al. 2006; Ting-Qiang et al., 2006). Nonetheless, information pertaining to cell wall-beryllium detoxification mechanism has not been studied in planta therefore future studies should be focused to consider this aspect.

#### 7. Beryllium compartmentalization in the vacuole

The vacuole is an important storage site in plants and plants used them to sequester toxic ions as stress adaptive mechanism. Vacuolar compartmentalization of beryllium could be a very important trait however no mechanism has been identified so far. One possible assumption could be that the sequestration of beryllium in vacuole could be driven by the pH gradient across vacuolar membranes (Fig. 3). However, Gries and Wagner (1998) reported that pH gradient was not the only reason for vacuolar sequestration of Ni in Ni sensitive oat seedlings. Another important transport system (V-ATPase) localized on tonoplast may also play very crucial role in the sequestration of beryllium in vacuole, and subsequently may reduce beryllium toxicity in cytosol (Fig. 3). However this mechanism has yet to be examined.

Based on similar properties of beryllium with other elements, another mechanism can be proposed, which involves the role of chelators in beryllium accumulation. Initially, beryllium ions might be mobilized by the action of chelators, which would be followed by uptake of beryllium-chelate complex via different transport system across the plasma membrane. Upon reaching leaf apoplast, those chelated beryllium complexes would be sequestered in the vacuoles. Future research is required to examine the mechanism behind beryllium sequestration in the vacuole. Identification of key transporters in transporting beryllium from apoplast to symplast and sequestration in vacuole would be very useful in developing beryllium stress tolerance plants.

#### 8. Beryllium compartmentalization in epidermal bladder cells

Compartmentalization of toxic ions in bladder cells is an important feature of halophytic plants and helps plants to cope with stress in different manners (Flowers and Colmer, 2008; Ishida et al., 2008). Extensive literature is available regarding the role of salt bladders and salinity tolerance mechanism in different plant species (Agarie et al., 2007; Jou et al., 2007; Shabala and Mackay, 2011) however it has never been considered under beryllium stress. Under salt stress enhanced sodium accumulation in the vacuoles of salt gland correlate with high tonoplast  $Na^+ / H^+$  antiport and  $H^+$  -translocating ATPase (V-ATPase) activities (Barkla et al., 2002). Under beryllium stress, plant may store beryllium in bladder cells to store excess beryllium and save cell from beryllium toxicity (Fig. 3). Targeting these salt glands which are very important single cell models to study beryllium stress tolerance could be very beneficial. Furthermore molecular identity and modes of

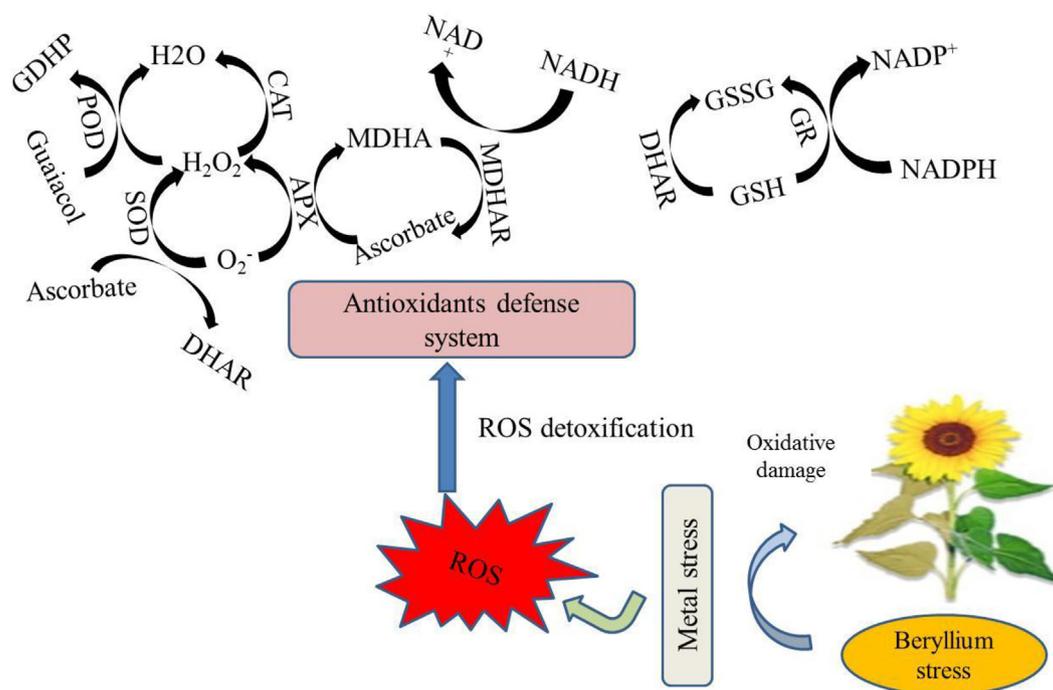


Fig. 4. Putative model of antioxidant defense system and their role in ROS scavenging under beryllium toxicity (extracted and modified from Tanveer et al., 2019).

control of key transport of beryllium in salt bladders are not identified yet, once identified it could be then used by plant breeders to modify the expression of other ion transporters in either stem epidermis or trichome-like outgrowths in traditional cereal crops such as wheat (*Triticum durum*) or barley (*Hordeum vulgare*).

## 9. ROS scavenging system

After the sequestration of excess beryllium in different storage compartments in cells, still plant has to cope with cytosolic beryllium toxicity. Under severe beryllium stress conditions, beryllium results in the production of free radicals (also known as reactive oxygen species-ROS), which may concomitantly alter redox potential at both intra/inter-cellular level (Agrawal et al., 2015; Shah et al., 2016). Singlet oxygen radicals under beryllium stress can generate different other reactive oxygen species, thus reduce plant growth and development under beryllium stress (Shah et al., 2016). Therefore it is imperative to improve beryllium tolerance in plants by reducing ROS production. This can be achieved by increasing antioxidant production (one possible solution) or by identifying plants with natural beryllium tolerance ability.

Engineering different enzymatic and non-enzymatic antioxidant can scavenge these beryllium induced ROS by converting them into O<sub>2</sub> and H<sub>2</sub>O (Fig. 4). Little information is available relating to antioxidant activity and ROS scavenging under beryllium stress in plants. It is well known that antioxidant production does not always consistent or directly proportional to severity in stress conditions, it also depends on study sample, sampling time, stress levels (Tanveer and Shabala, 2018). Hence it is more important to examine antioxidant activity under different conditions in plants in response to beryllium. In conclusion, targeting antioxidant defense system could be a potential source of beryllium stress tolerance in plants. Different strategies such as genetic engineering or MAS-based approach could be also used to increase the activity of antioxidants. This implies a need for a better understanding and developing tools for targeted regulation of plant redox systems in specific cellular compartments and tissues.

## 10. Conclusion

Beryllium is though non-essential element for plant, however, its high concentration results in significant plant growth reduction. Different mechanisms can be targeted to improve beryllium toxicity in plants. Among different targets, the role of transporters, sequestration in vacuole or bladder cells and role of cell wall could be primary beryllium detoxification mechanism while beryllium detoxification by antioxidants or by making complexes with ligands could be a secondary defense protocol. All these targets would be subjected to translational and transcriptional control, which should be identified in the future research. These processes would be varied among different plant species and therefore beryllium tolerant species should be identified and beryllium stress tolerance pathways should be highlighted using different genetic and biotechnological approaches.

## Contribution

M. Tanveer collected, compiled and wrote information. L. Wang polished the manuscript and gave useful suggestions.

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