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Mercury toxicity, molecular reaction and tolerance in plants: A review

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ABSTRACT

Cumulating of mercury in plants increase to the phytotoxicity and impairs numerous metabolic processes, including nutrient uptake, water status, and photosynthesis. Contamination of mercury in soils has become a great concern because of its natural release and anthropogenic activities. This research understanding the speciation of mercury, transformation, and transportation and toxicology tolerant regulation in plants, and minimization strategy, introducing the sources of mercury contamination in soils. Mercury ($Hg^{)}$ exists in different forms, ionic mercury (Hg^{+2}) is the predominant form in soils and readily absorbed by plants. Uptake, transport, and localization of mercury (Hg^{+2}) in plants that induce phytotoxicity and damage considerable metabolic processes. Mechanisms of mercury-induced toxicology, molecular response and gene networks for regulating plant tolerance. Extremely advance has been made in profiling of transcriptome and more importantly, uncovering a group of small RNAs that potentially mediates plant tolerance to mercury (Hg^{+2}). Recently discovered several signaling molecules such as nitric oxide and carbon monoxide have described as the regulators of plant tolerance to mercury (Hg^{+2}). Major importance to understand the extent of the toxicity in plants and animals and the consequences from the ingestion of contaminated food. Mercury (Hg^{+2}) is easily modified into several oxidation states, and it can be spread in many ecosystems. Due to the recurrence of mercury (Hg^{+2}) pollution and due to the lack of knowledge about the effects of this heavy metal in plants. The aim of this research is to provide a comprehensive review of the literature regarding mercury (Hg^{+2}) phytotoxicity.

Keywords: mercury, plant, nutrient uptake, water status, contamination, transformation, transportation, toxicology

1. Introduction

Pollution of heavy metals, as a global problem affecting the terrestrial and aquatic environments, as well as posts a potential threat to human health through the food chains. Meantime excessive concentrations of heavy metals in soils gradually resulted in yield reduction and poor quality of crop products. Suszcynsky and Shann (1995) stated that mercury considers as one of the most toxic heavy metals because of its easy bioaccumulation in living bodies, which can enter to the agricultural soil through various anthropogenic activities including fertilizers, pesticides, sludge, lime and manure Fig.(1).

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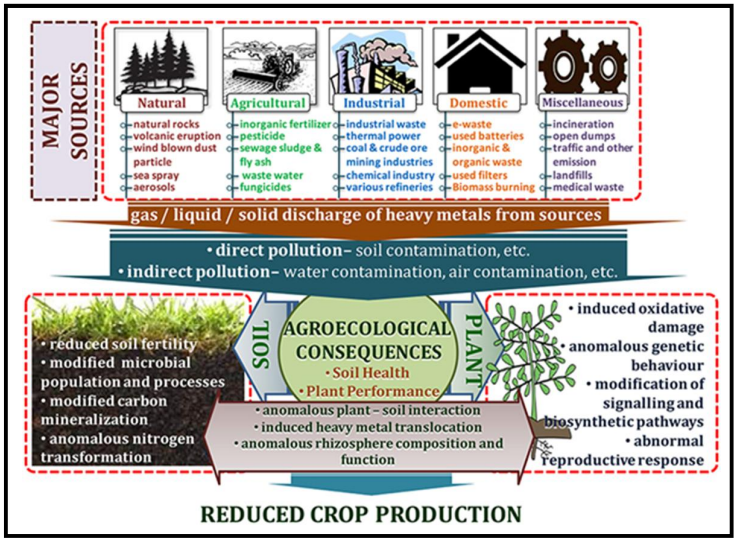

Fig. 1: Overview of sources of heavy metal pollution and its agro ecological consequences. After: Srivastava *et al.* (2017)

Srivastava *et al.* (2017) stated that heavy metal (HM) contamination has become a prime concern for today's society because of modern urbanization and industrialization. The impacts of heavy metals contamination particularly, on agriculture lands to the produce in our food basket should be considered. Heavy metals (HMs) and metalloids, including Cr, Mn, Co, Ni, Cu, Zn, Cd, Sn, Hg, Pb, among others, can result in significant toxic effects. Intensification of agricultural land use and changes in farming practices along with technological advancement have led to heavy metal pollution in soil. Metals /metalloids concentrations in the soil are increasing at alarming rate and affect plant growth, food safety, and soil microflora. The biological and geological reorganization of heavy metals depend chiefly on green plants and their metabolism. Metal toxicity has direct effects to flora that forms an integral component of ecosystems. Alternation of biochemical, physiological, and metabolic processes are found in plants growing in regions of high metal pollution. However, metals like Cu, Mn, Co, Zn, and Cr are required in trace amounts by plants for their metabolic activities. The present review aims to catalog major published works related to mercury contamination in modern day agriculture, and draw a possible road map toward future research in this domain.

Mercury exists in nature in forms of ionic mercury, methyl mercury, and mercury sulfide and mercury hydroxide. Han *et al.* (2002), Heaton *et al.* (2005) reported that ionic mercury is the predominant toxic form. Toxic action of mercury is done on the roots, which take up mercury directly in an efficient manner Han *et al.* (2006). Mercury may bind to the water channel proteins of root cells and thus, causes physical obstruction to water flowing, consequently, affects the transpiration in plants when entering the root cells, Maggio and Joly (1995), Zhang and Tyer man (1999).

Sapre *et al.* (2019) stated that the organic forms of mercury roughly affects plants, as they are more toxic than inorganic forms (Hg^{2+}) Patra and Sharma (2000). Toxic effect of mercury on most of the crop species, beyond the tolerance limit. It tends to a mass in the roots; hence, the phytotoxic symptoms are also noticed in roots Chen *et al.* (2014). Plants, causing disorders and fail to many of the biological processes, including photosynthesis, respiration, transpiration and cell division, take up the excess of mercury in the soil. Fig. (2).

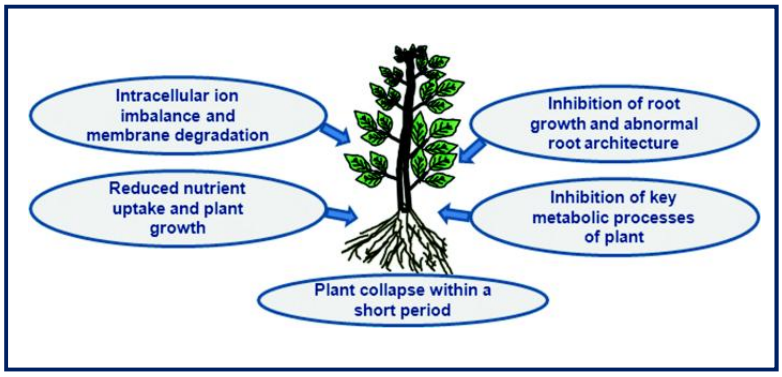

Fig. 2: Illustrates the effects of mercury toxicity on plants After: Sapre *et al.* (2019).

The mechanism of mercury toxicity is its ability to react with the sulfhydryl (SH) groups of proteins and enzymes; similarly, it has high affinity for the phosphate groups of lipids, energy-rich molecules such as ATPs and nucleotides, it also substitutes the essential ions such as Mg^{2+} ion in chlorophyll Azevedo and Rodriguez (2012). Mercury also messes up with the aqua-porins (water channels), causing impaired transpiration and subsequent water uptake via vascular tissues Zhou *et al.* (2008). It carefully disrupts the plant antioxidant defense enzymes, especially, glutathione reductase (GR), superoxide dismutase (SOD), and catalase and ascorbate peroxidase (APX). Besides, it also affects the other antioxidant entities such as glutathione (GSH) and non-protein thiols Israr *et al.* (2006), Zhou *et al.* (2008). The plants can tolerate the effect of mercury toxicity to some extent by the interplay of various physiological and molecular mechanisms. First, when plants are exposed to mercury ions, they prohibit or reduce the uptake of mercury into the roots by either complexing them to cell wall or root exudates; when enters the root cell, the metal ion is restricted to the apoplasts. Nevertheless, if mercury ions gain entry into the plant cell, they are countered by detoxification through compartmentalization into vacuoles or complexation with amino acids, organic acids, chelation by phytochelatins (PC) and metallothioneins (MT). Furthermore, some of non-enzyme antioxidants such as a-tocopherol and GSH also aid in combating mercury toxicity Kalaivanan and Ganeshamurthy (2016). Rascio and Navari-Izzo (2011) stated that such process mostly put a check on translocation of mercury ions to the leaf tissues and thereby, shielding the photosynthesis from detrimental effect of mercury. Finally, plants resort the mercury toxicity by induction of the oxidative stress enzymes such as SOD, APX, catalase, glyoxalase and GR. They also trigger the stress-responsive proteins and hormones. Various signaling are stimulated by encountering heavy metal ions, namely calcium-dependent signaling and mitogen-activated protein kinase (MAPK) signaling Tiwari and Lata (2018). Recently, mercury toxicity activates the biosynthesis of aromatic amino acids (tryptophan and phenylalanine), calcium accumulation and stimulates mitogen-activated protein kinase (MAPK) in rice Chen *et al.* (2014).

Mercury suppresses photosynthesis, chlorophyll synthesis, as well as uptake and transport of nutrients. Mercury is considered to inhabit the activity of the NADPH: protochlorophyllide oxidoreductase (POR) that plays important roles in photosynthesis, consequently, affects plant growth involving in biomass Lenti *et al.* (2002). Sahu *et al.* (2012) evaluated the oxidative damages response to mercury concentrations in wheat, represent lower and higher mercury concentration induced and repressed antioxidant enzymes activities separately, which supported the opinion that mercury can boost the formation of reactive oxygen species (ROS) and consequently, post more serious oxidative stress on plant cell. Mercury used primarily in gold mining, batteries, paints, pesticides, impregnation of wood and electrical products. Because of its enormous use, this metal is accumulated at various sites and reflected as a global pollutant Kabata-Pendias, (2011). Plants take up mercury directly depends on its quantities in the soil. Mercury not only accumulated from the soil by plants, but also immersed in progressively released mercury (Hg^{2+}) vapor from the soil Israr *et al.*, (2006).

High accumulation of mercury (Hg^{2+}) in roots may inhibit plant uptake of K^{+}. However, lower volume of mercury (Hg^{2+}) gradually stimulate K^{+} uptake. It is known that the toxicity of volatilized

elemental mercury (Hg^{2+}) is the most serious for plants. McNear *et al.*, (2012), reported that increasing the production of ethylene, mercury (Hg^{2+}) vapor induces processes related to senescence, and (Hg^{2+}) is the most active toxicant not ionic form. More than developed plants, young plants are more sensitive to mercury (Hg^{2+}) saturated air. Mercury has a strong affinity with multiple proteins and enzyme amino acids. Zhou *et al.*, (2008) stated that binding nature of mercury to sulfhydryl groups is the key reaction to plant metabolism disruption with Se in soybean root molecules of high molecular weight. In addition, improved antioxidant enzyme activity is observed in some cases when mercury is applied to growth media.

Many studies showed that mercury (Hg^{2+}) showed inhibition effects on growth Mishra and Choudhuri (1999), chlorophyll biosynthesis Singh *et al.* (2021), Matson *et al.* (1972), and activity of photosynthesis of plants and phytoplankton Deng *et al.* (2013), Matorin *et al.* (2009), Protopopov *et al.* (2021). Most studies investigated the adverse effects of mercury (Hg^{2+}) on photosystem II (PSII) activities, located in the donor and/or the acceptor sides and the reaction center of PSII of plants Ahmad *et al.* (2022), Patra *et al.* (2004) Fig. (3). Wang *et al.* (2022) stated that mercury (Hg^{+2}) poses high toxicity to organisms including algae. Studies showed that the growth and photosynthesis of green algae such as *Chlorella* are vulnerable to (Hg^{+2}) stress. However, the differences between the activities and tolerance of photosystem I and II (PSI and PSII) of green microalgae under Hg exposure are still little known. Responses of quantum yields and electron transport rates (ETRs) of PSI and PSII of *Chlorella pyrenoidosa* to 0.05–1 mg/L (Hg^{+2}) were simultaneously measured for the first time by using the Dual-PAM-100 system. The photosystems were isolated to analyze the characteristics of toxicity of Hg during the binding process. The inhibition of Hg^{2+} on growth and photosystems was found. (Hg^{+2}) more seriously affected PSII than PSI. After (Hg^{+2}) exposure, the photochemical quantum yield of PSII [Y (II)] decreased with the increase in non-photochemical fluorescence quenching [Y (NO) and Y (NPQ)]. The toxic effects of (Hg^{+2}) on the photochemical quantum yield and ETR in PSI were lower than those of PSII. The stimulation of cyclic electron yield (CEF) was essential for the stability and protection of PSI under Hg stress and played an important role in the induction of non-photochemical quenching (NPQ) The results showed a strong combination ability of (Hg^{+2}) ions and photosystem particles. The number of the binding sites (n) of (Hg^{+2}) on PSII was more than that of PSI, which may explain the different toxicity of (Hg^{+2}) on PSII and PSI.

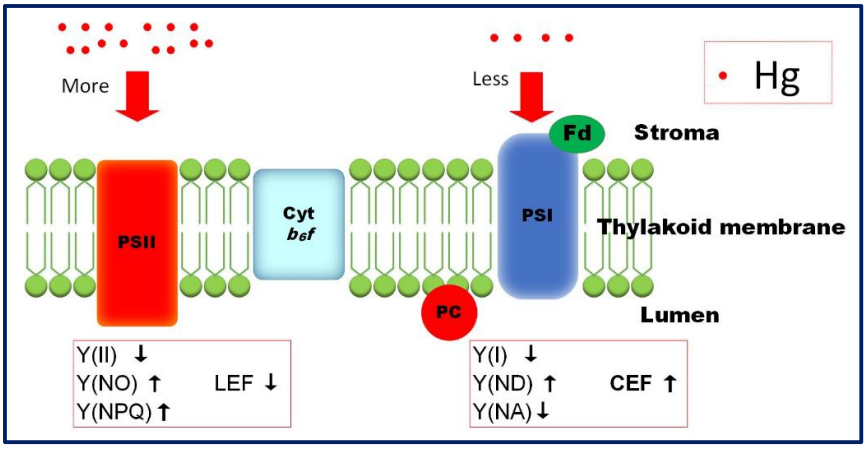

Fig. 3: Illustrates the abinding ability of mercury (Hg^{+2}) to photosystems, I and II explained the difference in toxicity After: Wang *et al.* (2022)

Deng *et al.* (2013) reported that photosystem I (PSI) activity could be reduced under the stress of mercury (Hg^{2+}). However, the effects of heavy metals on PSII and PSI are separately studied in most studies. Moreover, the differences between the activities and tolerance of PSII and PSI in intact algal cells under Hg exposure are also little known. Therefore, Klughammer, and Schreiber (2008) stated that a Dual-PAM-100 system was used to reflect the physiological status of PSII and PSI under mercury (Hg^{2+}) toxicity, which showed its advantage in simultaneous measurements of chlorophyll a fluorescence and P700+ absorbance changes of intact cells. In addition, some heavy metals were

reported to stimulate the cyclic electron flow (CEF) around PSI Wang *et al.* (2013). These studies showed that the cyclic electron flow (CEF) played an important role in coping with abiotic stress and protecting PSI. However, whether the cyclic electron flow (CEF) was stimulated under mercury (Hg^{2+}) stress, and the response and physiological function of the cyclic electron flow (CEF) around PSI under mercury (Hg^{2+}) stress still need further studies. The toxic effects of inorganic mercury (Hg^{2+}) on the activities of PSII and PSI of green microalga *Chlorella pyrenoidosa* were studied. The green microalgae, such as *C. pyrenoidosa* used in the study, are the main primary producers and essential in food chains in aquatic ecosystems, and *C. pyrenoidosa* has often been used as a model microbial species for examining the effects of contaminants on photosynthesis Wang *et al.* (2013), Li *et al.* (2021). Cyclic electron flow (CEF) around PSI and non-photochemical fluorescence quenching, which provided protection to photosynthetic apparatus under stress, were also tested to show the effects of Hg^{2+} on the regulation of electron transport and energy usage or dissipation. Assuming that the toxicity of heavy metals in photosynthesis was related to their binding abilities to photosynthetic apparatus, so the binding features of mercury (Hg^{2+}) ions and photosystem particles were detected to explain the different toxicity of mercury (Hg^{2+}) on PSII and PSI. The mechanisms of mercury-induced toxicology, molecular response and gene networks for regulating plant tolerance will be discuses.

2. Mercury speciation, transformation, and transportation

WHO (2017) reported that mercury contaminated soils pose a risk to global public health, with Hg being listed as one of the 'ten leading chemicals. In 2013, the United Nations (UN) introduced the 'Minamata Convention on Mercury', which aims for a more global effort in managing the risk of Hg to human health and the environment. Signed by 128 countries UNEP, (2016), it entered into effect in 2017, Selin *et al.*, (2018). Obrist *et al.*, (2018) stated that global amount of Hg mass accumulated in soils is very large; assumed to be in the range of 250–1000 Gg. Although Hg occurs naturally in soils from geologic sources, through natural events such as forest fires and volcanic eruptions. Ermolin *et al.*, (2018) stated that significant proportion of that Hg is attributed to anthropogenic influences, with an estimated 86 Gg of anthropogenic, UNEP, (2009). Wallschläger, (1996) stated that mercury emissions gradually accumulated in surface soils.

The chloralkali process has brought about anthropogenic mercury pollution, cement production, mining and smelting, artisanal small-scale gold mining, coal burning, and oil refining, which together emit huge quantities of Hg to the environment Science Communication Unit, (2013), on the order of 2 Gg per year UNEP, (2009). Mercury contamination has become a global environment problem because millions tons of mercury have been released to ecosystems due to anthropogenic activities. Since 1500, approximate one million tons of metallic mercury has been extracted from cinnabar and other ores Hylander and Meili (2003). Han *et al.* (2002) reported that in 2000, the average mercury level in global arable lands was 39 kg km^{-2}. However, mercury was released from the following sources, (**a**) applying as an amalgamation agent for extracting silver and gold and (**b**) red mercury mines were explored for producing cinnabar and pigment Hylander and Meili (2003). Due to the industrialization (e.g. chlor-alkali industry and coal burning), global mercury release increases remarkably Sznopek and Goonan (2000), Kolker *et al.* (2006). Coal fired power plants, metal smelters and other industries contribute approximately a quarter of the world annual total Hg emissions to the atmosphere Larssen (2010); Wu *et al.* (2006).

Our understanding of the critical processes driving global mercury (Hg) cycling, in particular those that affect large-scale exchange of Hg among major environmental compartments, has advanced substantially over the past decade. Major advances in three interconnected areas have driven progress: new data, new models, and new analytical tools and techniques. Summarizing the state of knowledge of the major global Hg reservoirs in the Earth system: the atmosphere, terrestrial ecosystems, and aquatic ecosystems, describing the constraints on processes that control Hg exchanges between these reservoirs, and the relative influences of policy, land use, climate change, and anthropogenic disturbances on Hg cycling Fig. (4).

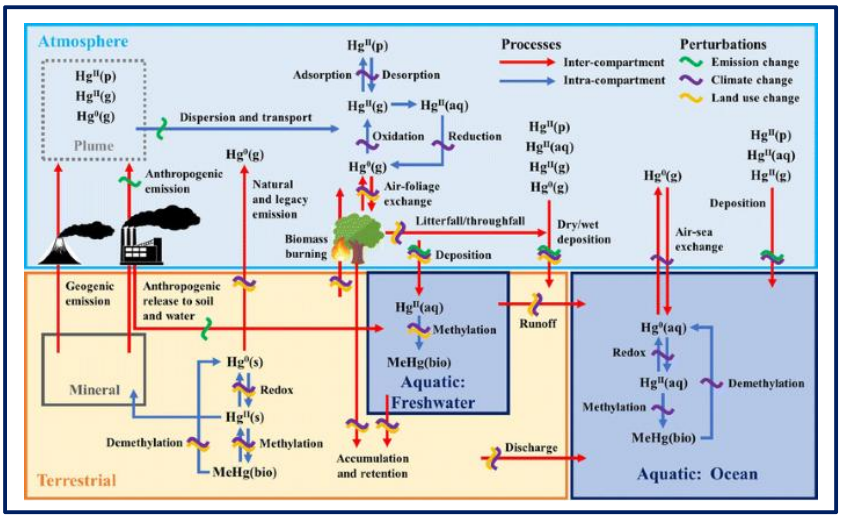

Fig. 4: Illustrates the critical processes of global importance for Hg cycling, including fluxes between major environmental compartments. Perturbations of Hg processes and fluxes show anticipated impacts due to changes in emission, climate, and land use. After: Obris *et al.* (2018)

Analyses of newly available data in the context of advances in modeling capabilities and novel analysis techniques have improved our understanding of fundamental processes relevant to Hg cycling. In the past decade, new data have become available from areas of the world where they previously were lacking, including Asia, the tropics, and the southern hemisphere. Environmental models are increasingly used for synthesizing global observations and describing the mechanisms driving Hg speciation, cycling, and bioavailability. Global three-dimensional (3D) models of Hg in the atmosphere Durnford *et al.* 2012; Bieser *et al.* (2017), Horowitz *et al.* (2017), terrestrial ecosystems Smith-Downey *et al.* (2010), and oceans Zhang *et al.* (2014), (2015b); Semeniuk and Dastoor (2017) have improved our understanding of Hg processes.

A major advance has been the development of a hierarchy of modeling tools that collapse the necessary detail from global simulations into more computationally feasible geochemical box models, enabling fully coupled simulations of the interactions among the land, atmosphere, and oceans over millennial time scales Amos *et al.* (2013), (2014), (2015). When combined with information on the cumulative history of human Hg release from antiquity to the present, this modeling approach has revealed a much greater contribution of human activity to the global Hg cycle than previously recognized Streets *et al.* (2011), (2017). The last 10 years has also seen rapid development in Hg stable isotope biogeochemistry, providing a valuable tool to quantify Hg sources and study transformation processes Sonke (2011), Sun *et al.* (2016a). These recent advances have proven particularly valuable for investigating the anticipated impacts of human and natural perturbations on global Hg cycling. Changes in anthropogenic emissions are ongoing and will continue into the future, including strong shifts in global source areas compared to current emission patterns Giang *et al.* (2015). Accelerating land use and climate change are expected to have significant effects on global, regional, and local Hg cycles, with unexpected feedbacks and nonlinear impacts on Hg exposure. Models have been applied to assess the impact of regulatory interventions, such as emission controls Selin *et al.* (2018), on specific outcomes and to evaluate policy efforts to mitigate Hg pollution Selin (2014). An increasing number of studies are now available documenting such changes.

The atmospheric mercury (Hg), which undergoes oxidation reactions and deposits to the ground, increases the abundance of mercury (Hg) in soils and waters Lindberg *et al.* (2007). Additionally, considerable amounts of mercury introduced into agricultural soils in the forms of mercury-containing compounds such as fertilizers, pesticides, lime, manures, and soil amendments contribute a great deal to mercury contamination Han *et al.* (2002), Heaton *et al.* (2005); Han *et al.* (2006), Huang *et al.* (2011).

Chemical forms of mercury (Hg) in soils can include elemental Hg(0), Hg in sulfide minerals (e.g., metacinnabar, β-HgS), Hg chlorides (e.g., calomel, Hg_2Cl_2), inorganic Hg(II) adsorbed to surfaces of clay minerals, iron (oxyhydr)oxides, or soil organic matter (collectively referred to as "matrix-bound

Hg(II)", and methylated Hg species (MeHg). Of particular importance are the presence and quantities of Hg (0) and MeHg. The presence of Hg (0) could lead to elevated gaseous Hg emissions to the surrounding atmosphere Obrist *et al.* (2014), especially during soil remediation works, and to losses of Hg during the sampling and sample preparation for soil analyses Schwab *et al.* (2002). In general, Hg in soils and sediments is controlled by inorganic and organic interactions, since it has an affinity to Cl^{-}, OH^{-}, S_2^{-}, and S-containing functional thiol groups in organic ligands Gabriel and Williamson (2004), Skyllberg (2011). Organic matter can mobilize and immobilize Hg, depending on the prevailing soil pH and redox potential Poulin *et al.* (2016), Yin *et al.* (1997). In addition, in well-oxygenated soils, Hg can be mobilized by the presence of high concentrations of Cl^{-} ions Kim *et al.* (2004) that act as a complexing agent, and conditions potentially found in areas with high usage of road deicing salts Charlet *et al.* (2017). Furthermore, soil water is often dominated by Ca^{+2} ions, especially in carbonate-bearing and other circum-neutral soils. The Ca^{+2} concentration can influence Hg mobility either by competing for sorption sites with Hg (II), or by promoting the aggregation of Hg-bearing colloids, that reducing Hg mobility Ravichandran *et al.* (1999). In soils with variable redox conditions, sulfide can compete with thiol groups of organic matter and precipitate Nanoparticulate HgS in the form of metacinnabar (β-HgS) Gerbig *et al.* (2011), particularly in contaminated soils Barnett *et al.* (1995), Barnett *et al.* (1997). Generally, HgS is stable and has a low solubility Drott *et al.* (2013), though a number of different parameters can affect this. The nanoparticles formed in situ in soils can be stabilized by organic matter Deonarine and Hsu-Kim (2009), but will be structurally disordered when formed in low sulfidic environments Poulin *et al.* (2017), and may be more bioavailable for Hg methylation the most toxic form of mercury Graham *et al.* (2012), Zhang *et al.* (2012), Clarkson and Magos (2006). Under reducing conditions, the formation of MeHg is predominantly a biotic process, formed by both sulfate-reducing and iron-reducing bacteria Barkay and Wagner-Dobler (2005). While MeHg is not a major species in predominantly aerated soils, its extreme toxicity is highly relevant for risk assessment. Unfortunately, the study of solid-phase Hg speciation in soils is not a straightforward task. Various extraction-based techniques have been developed to divide Hg-species into "operationally-defined" pools, but they can be prone to artifacts Bloom *et al.* (2003), Reis *et al.* (2016). More direct information about the dominating Hg species in soils can be obtained by synchrotron X-ray absorption spectroscopy (XAS) with linear combination fitting analysis based on known reference compounds; however, this technique requires high Hg concentrations and has its limitations. Another technique is thermal desorption analysis (also known as pyrolysis with Hg detection), which is very effective in detecting the presence of elemental Hg(0) in soils or sediments, but other relevant species that are common in soils are difficult to discriminate from each other, due to overlapping Hg release curves Reis, *et al.* (2015). MeHg analyses require special extraction procedures and analysis by high-performance liquid chromatography (HPLC) or gas chromatography (GC) coupled to inductively coupled plasma mass spectrometry (ICPMS). Thus, characterization of the chemical speciation of Hg in soils and sediments requires a combination of multiple methods.

3. Immobilization processes of Hg in soil

Immobilization of Hg in soil through HgS complex formation, the anoxic conditions or highly oxidizing conditions of rhizospheres enhance microbial activity, decrease pH, and promote the release of carbon-rich root exudates that can facilitate the formation of sulfides (S^{2-}) Jia *et al.* (2015). Mercury (Hg^{2+}) ion is a class B metal ion with a strong affinity for ligands with soft donor atoms Rayner-Canham and Overton (2010). Mercury (Hg^{2+}) tends to form stable complexes with OH^{-}, Cl^{-}, and S containing functional groups of organic ligands Powell *et al.* (2004), Fig. (5). Ping, (2016), reported that mercury (Hg) is a global contaminant of ecosystems and human health risk, with complicated biogeochemical processes. Mercury sulfide (HgS) dissolution has been suggested as a key process in Hg cycling, as it could potentially increase the pool of inorganic Hg (i Hg) for the production of methyl mercury (MeHg). Considering the lack of feasible techniques to differentiate dissolution and re-adsorption processes, under such condition, tracer technique was used (isotope dilution techniques) in order to investigate the re-adsorption of released Hg during HgS dissolution. The HgS dissolution rate with consideration of re-adsorption was two times the rate calculated from detecting Hg alone in the presence of O_2, indicating the importance of Hg re-adsorption during HgS dissolution. Furthermore, examine the role of Hg-ligand complexation in HgS dissolution and Hg(II) re-adsorption using the thermodynamic adsorption method,

selecting L-cysteine (Cys) as a model compound for low molecular weight ligands and fulvic acid (FA) for natural dissolved organic matter (DOM).

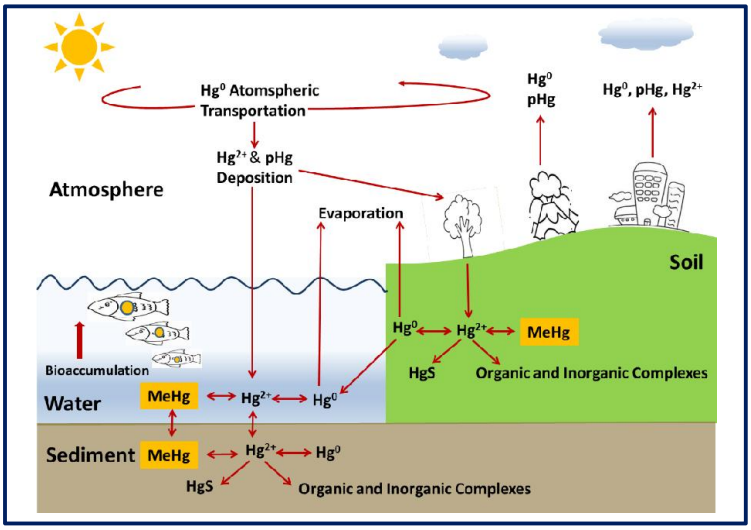

Fig. 5: Illustrates the biogeochemical cycling of mercury in the environment.
After: Ping, (2016).

The presence of Cys may enhanced the dissolution of HgS through decreasing the re-adsorption of Hg-Cys complex, however, FA inhibited HgS dissolution, due to the adsorption of FA on HgS surface that covered dissolution sites. The geochemical modeling method to study the Hg speciation and the relation of inorganic mercury (i Hg) speciation to MeHg, aiming to provide a methodological example for potentially evaluating the implications of Hg species distribution during HgS dissolution on MeHg production. Modeling results suggest that sulfide and DOM govern inorganic mercury (iHg) speciation, and the Hg-sulfide and Hg-DOM species are related to MeHg in environment, suggesting the importance of inorganic mercury (iHg) speciation in MeHg production and the complexity of Hg bioaccumulation. Barnett *et al.* (1997) noticed that mercury can form HgS upon binding with – SH groups of organic matter that exists at a higher redox potential than S^{2-}. The affinity of Hg^{2+} for S^{2-} results in the formation of mercuric sulfide precipitation (HgS) low solubility complex, as follows: $Hg^{2+} + S^{2-} \rightarrow$ HgS Boszke *et al.* (2006), Jonsson *et al.* (2012).

Mercury immobilized in soil through forming HgSe inert complex formation. Selenium often occurs as an isomorphous substituent of sulfur (S) in sulfide crystal lattices. In addition, S and Se have the same atomic structure, the same charge (S^{2-} and Se^{2-}), and similar atomic radii and ionic radii (S: 0.184 nm, Se: 0.191 nm); thus, Se can easily be incorporated into the crystalline lattices of S Zhang, (2014b). Therefore, S^{2-} can be replaced by Se^{2-} to form inert mercuric selenide (HgSe) precipitates or an isomorphous series of HgS–HgSe (in cinnabar ore), because the binding affinity of Se^{2-} with Hg (logK 10^{45}) is one million times greater than that of S with Hg (logK 10^{39}) Syversen and Kaur (2012), Zhang *et al.* (2014). Moreover, the solubility product constants of HgSe precipitates ($^{K}sp \sim 10^{-58}$–10^{-65}) are drastically lower than those of HgS precipitates ($^{K}sp \sim 10^{-52}$) Björnberg *et al.* (1988). When Se and Hg coexist in soil under appropriate conditions, Hg can first thermodynamically react with Se to form an inert, highly stable HgSe precipitate Fig. (6). Se may thermodynamically react with Hg^{2+}/Hg0 to form an insoluble HgSe complex in the rhizosphere Yang *et al.* (2008); McNear *et al.* (2012), as presented in the following chemical equations: $Hg^{0} + Se^{0} \rightarrow$ HgSe and/or $Hg^{2+} + Se^{2-} \rightarrow$ HgSe.

Mercury immobilized in soil through forming organo-HgSe complex processes. In addition, inert HgSe complex, organic HgSe complexes are also found in paddy soil, with Se, Se may displace S in the R-SH, R-SSH, and R-SS-R groups to form more stable chemicals, such as R-SeH, R-Se SeH, and R-Se Se-R Khan and Wang (2009).

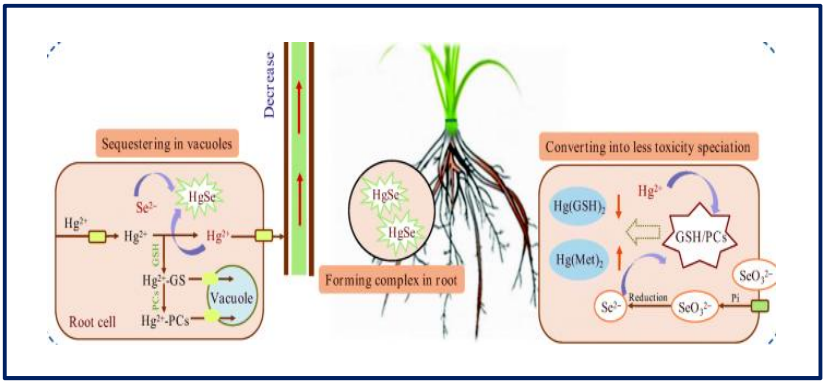

Fig. 6: Illustrates the mechanisms underlying Hg detoxification in soil–plant systems after Se application. After: Tran *et al.* (2021)

Simultaneously, Hg binds to non-R-SH, R-SSH, and R-SS-R and may be released and reabsorbed by strong Se functional groups Laurier *et al.* (2003); Shoham-Frider *et al.* (2007), thereby forming strong complexes with Se-organic ligands, which are more inert and stable and less available to microbes and plants. Xu *et al.* (2019). Further suggested that HgSe in soil might contain HgSe, CH_3HgSe^-, and $(CH_3Hg)_2$ Se, as well as HgSeR, RSHgSeR, CH_3Hg-SeR, and CH_3Hg-SeSR, which play dominant roles in soil Hg levels. However, this finding needs to be verified further. Promotion of Hg immobilization in soil Wang *et al.* (2016b) demonstrated that Se^{2-} could react with Hg^{2+} under anoxic and suboxic conditions and form HgSe complexes, despite sulfate input in paddy soil. They also found by transmission electron microscopy and energy dispersive X-ray spectroscopy that the molar ratios of Hg: Se and Hg: S were 1 in nanoparticles. However, another study showed that Hg LIII-edge synchrotron radiation X-ray absorption near-edge structure (XANES) spectrum exhibited that the typical spectral feature was HgSe instead of α-HgS Wang *et al.* (2016a). Zhang *et al.* (2012) found that Se contents were positively correlated ($P < 0.01$) with Hg contents in flooded soil due to the formation of HgSe complexes in the rhizosphere. Other studies reported that application of SeO_3^{-2}, or SeO_4^{-2} to dry land soil promoted the formation of HgSe precipitate in the rhizospheres of radish (Raphanus sativus L.) Shanker *et al.* (1996b), tomato (*Solanum lycopersicum L.*) Shanker *et al.* (1996a), or pak choi (*Brassica Rapa L.* var. Chinensis) Tran *et al.* (2018a). In addition, HgSe compounds may react further with dissolved organic matter in the rhizosphere to form high molecular weight HgSe complexes Plant *et al.* (2003); Chiasson-Gould *et al.* (2014).

4. Interactions of mercury (Hg) and soil

Obrist *et al.*, (2018) reported that pedosphere is deemed a net sink of Hg, primarily due to Hg taken in by plants being deposited on soils. Current global Hg models suggest that land surfaces receive 3200 Mg yr^{-1} through atmospheric deposition and re-emit 1700 to 2800 Mg yr^{-1}, illustrating the dual role of soils in global Hg cycling as sink and source for atmospheric mercury (Hg). After long-range transport, atmospheric Hg (0) is oxidized and deposited directly onto soils with precipitation or indirectly via plant surfaces with through fall. Gaseous Hg (0) is also can be taken up plants through stomata, which oxidized in the plants, and deposited onto soils through litter fall, or directly deposited from the atmosphere to terrestrial surfaces as dry deposition. In soils, Hg (II) may be methylated or reduced to volatile Hg (0) which is eventually re-emitted back to the atmosphere Fig (7)

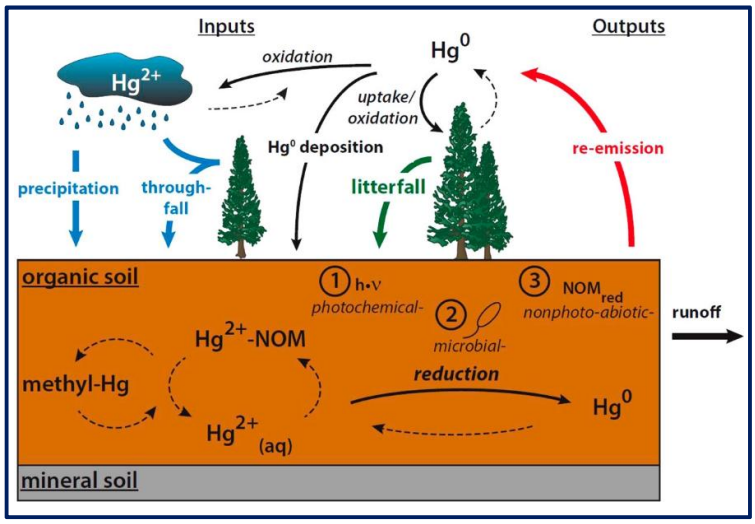

Fig. 7: Illustrates the conceptual model of the terrestrial Hg cycle: Major input and output pathways. Atmospheric Hg is mainly deposited as oxidized Hg (II) via precipitation and through fall or taken up by plant stomata and deposited with litter fall. In soils, different pathways can reduce Hg (II): (1) photochemical, (2) microbial, or (3) nonphotochemical abiotic reduction by natural organic matter (NOM), followed by re-emission back to the atmosphere. All Hg forms are subjected to leaching from soils with surface or subsurface runoff into aquatic ecosystems. After: Jiskra *et al.* (2015).

Jiskra *et al.* (2015) stated that soils comprise the largest terrestrial mercury (Hg) pool in exchange with the atmosphere. To predict how anthropogenic emissions affect global mercury cycling and eventually human mercury exposure, it is crucial to understand Hg deposition and re-emission of legacy mercury from soils. Results showed that mercury in the soils was dominantly derived from deposition of litter (~90% on average). However, remaining fraction was attributed to precipitation-derived mercury, which showed increasing contributions in older, deeper soil horizons (up to 27%) indicative of an accumulation over decades. We provide evidence for significant mercury re-emission from organic soil horizons most likely caused by nonphotochemical abiotic reduction by natural organic matter, a process previously not observed unambiguously in nature, suggesting histosols (peat soils), which exhibit at least seasonally water-saturated conditions, have re-emitted up to one third of previously deposited mercury back to the atmosphere. Re-emission of legacy mercury following reduction by natural organic matter may therefore, be an important pathway to be considered in global models, further supporting the need for a process-based assessment of land/atmosphere Hg exchange.

4.1. Adsorption of mercury to soil

Mercury (Hg) is known to be relatively immobile, as compared to many other metals in soil, as it can bind strongly with soil constituents. A number of studies have been carried out examining the competitive sorption and selectivity sequences of various heavy metals by various soils. Seo *et al.* (2008) explored the sorption potential of Hg and six other metals to a wetland soil. In batch mono-metal experiments (at pH=6), the seven metals were ordered by adsorptive capacity (mg/g) as follows: Pb (25.4) ≫Hg (6.4) > Cr (4.9) > Cd (2.9) ⩾ Cu (2.6) ⩾ Zn (2.4) ≫As (0.8). Based on multi metal adsorption they were ordered as Hg (3.0) > Cr (1.1) > Cu (0.6) ⩾ Cd (0.4) ≈Pb (0.4) ≫As (0.02) ≈Zn (0.02). Ignatavičius *et al.* (2022) stated that mercury is released into the environment in a variety of chemical forms by both geogenic and human activities, affecting the environmental conditions such as pH, redox potential, light and temperature-all of which determine its final chemical form-reactivity and toxicity. Methyl mercury is considered as one of the most poisonous forms, considering the methodologies of the studies carried out, illustrated the best technique for preserving methyl mercury in soil and sediment samples is to freeze it immediately after collection. Organically rich soils are related to higher total mercury levels. Solid-phase selenium causes faster demethylation and slower

methylation of mercury. Methyl mercury can increase by climate change and thawing; arctic permafrost is a potential source of Hg Fig. (8).

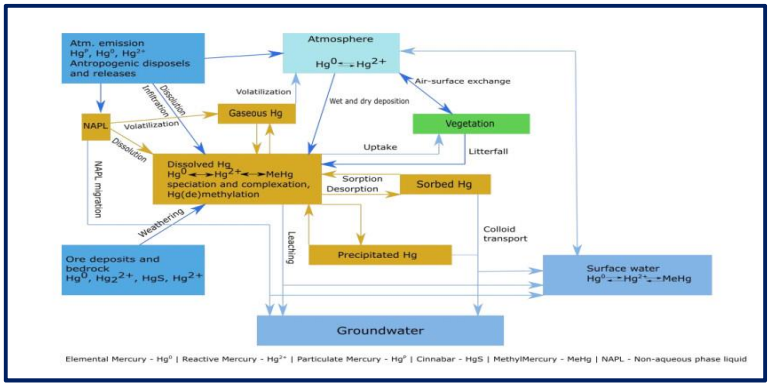

Fig. 8: Illustrates mercury sources, sinks, and phases in soil
After: Diederick (2013), Leopold *et al.* (2010) and Ignatavičius *et al.* (2022).

This research aims to communicate sampling methods, use and storage; it also focuses on mercury forms, mobilization and analysis in soil and sediment. The findings of this study are listed below:

- In the sampling method, different approaches depend on the chosen area, such as two-stage, cluster, judgmental, random, stratified random, systematic grid, and search and transect. Tools made of polymer, glass, stainless steel, or aluminum are required during the collecting, pre-treatment, and storage phases of environmental samples. The best technique for preserving MeHg is to freeze soil and sediment samples immediately after collection, followed by freeze-drying, grinding, homogenization, and storing the dry material in cold, dark conditions until analysis.
- Clay soils can absorb mercury and lead the creation of HgS.
- Organically rich soils, such as forest soils, peaty soils, or rice paddy fields are typically connected to higher THg concentrations.
- Mercury binding to humic substrates is the major process in mercury sorption.
- Plants can play an important role in mercury transport and accumulation. MeHg concentrations in biomass were found to be higher in *Solanum nigrum* (BR3) and *Cynodon dactylon* (BR2).
- It appeared that the adsorptive capacity of Hg is higher than Cr, Cd, Cu, and Zn and As but lower than Pb.
- Mercury can be affected by most of the conditions in the environment, such as pH, redox potential, and light.
- The soil profile, production of volatile mercury species, physical movement of Hg species, and physical and chemical sorption of mercury vapor all influence the depth of the soil layers that contribute to evaporation, as compared to unplanted regions, applying sulfur to the soil and growing a plant cover reduces mercury flow by around 70% to 80%.
- Shewanella one idensis MR-1 and *Geobacter spp* are two bacteria that can mediate the biotic reduction of mercury (Hg^{2+}) to HgO.
- The most common organic and toxic form of mercury in the environment is accepted as MeHg. Soil moisture highly affects MeHg, through sulfate and iron-reducing bacteria.
- A laboratory incubation analysis of surface lake sediments revealed that higher levels of solid-phase Se resulted in rapid demethylation and slower methylation of mercury and that the pH impact was varied owing to Hg availability and microbial activity.
- Climate change and permafrost thawing have the potential to increase MeHg production. Arctic permafrost represents an important source of mercury in case warming will not decrease in the future.
- In 2018, a simple and quick approach for analyzing MeHg utilizing chemical vapor generation inductively coupled plasma mass spectrometry was introduced. When compared to HCl, HNO_3 has proven to be the most effective for selective extraction of MeHg from soils. Ultrasonic agitation helped to produce rapid MeHg extraction.

The adsorption capacity for mercury remained strong in the presence of the other metals, whereas that for Pb was significantly lowered, Seo *et al.*, (2008). Antoniadis *et al.* (2017b) showed that mercury sorption was not related to the presence of any other potentially toxic elements at a highly contaminated former mining area in Germany. Liao *et al.* (2009) considered the adsorption of mercury in different types of soils, with Sharkey clay having greater mercury sorption capacity than Olivier loam soil, that was itself greater than Windsor sand. It was also revealed that mercury sorption in each case was rapid and strongly irreversible, with freely available mercury typically being<1%. The binding of mercury in soils is due to its tendency to bind with soil organic matter or soil matrix surfaces. Mercury can be regarded as an immobile metal in most soils due to highly stable complex formation Liao *et al.*, (2009), US EPA, (1997).

4.1.1. Adsorption of mercury to organic matter

Lehmann and Kleber, (2015), reported that soil organic matter is a system of progressively decomposing organic compounds being byproducts of the biogeochemical degradation of plants and animals. Organic matter consists of different types of substances such as high molecular-weight hydrophobic compounds, hydrophobic neutral organic matter, and low molecular weight compounds that are more hydrophilic Stevenson, (1994) Fig. (9).

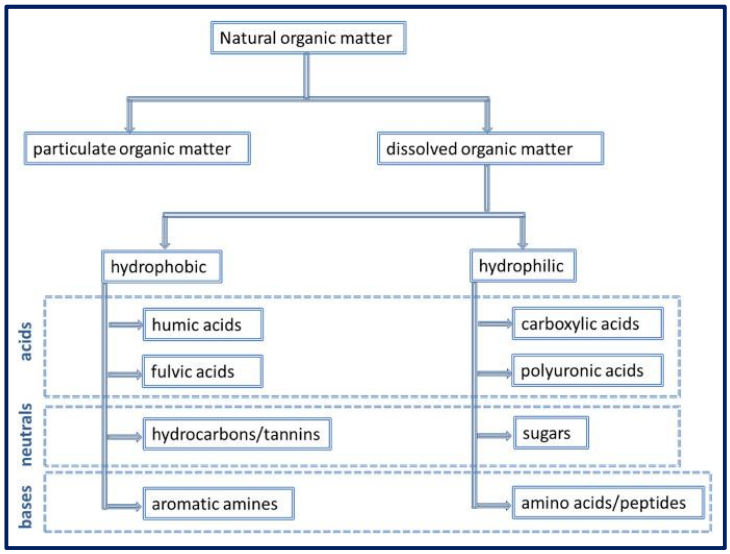

Fig. 9: Illustrates the characterization of organic matter.

Beckers and Rinklebe, (2017) reported that soil organic matter has a high affinity for mercury (Hg^{2+}), total mercury is often associated with organic rich soils, such as forest soils, peaty soils, or rice paddy fields. Mercury can bind to organic matter through functional groups, such as hydroxyl, carboxylic, aromatic and S-containing ligands may facilitate cationic Hg^{2+} binding Sysalova *et al.*, (2017) Fig. (10). Mercury in soil is particularly inclined to form covalent bonds with any available reduced S active sites Reis *et al.*, (2015b). Mousavi (2015) ascribed the reason for this to the phenomenon of polarizability. The hard and soft acids and bases rule predicts that soft acids and soft bases will have strong interactions. Because S containing thiol functional groups act as a soft base and Hg^{2+} is a polarizable soft acid, the binding is strong. Oxygen containing alcohol and carboxylic acid functional groups and N containing amine groups act as hard bases and, therefore, do not bind with Hg as strongly Fig. (10).

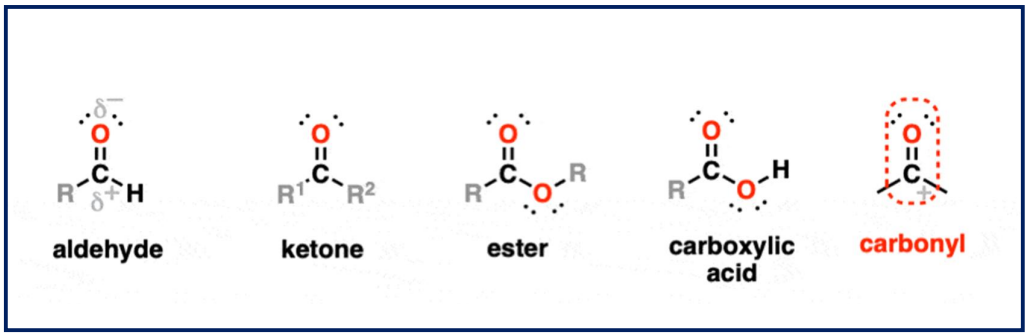

Fig. 10: Illustrates the functional group contains a carboxyl groupp- a carbon double-bonded to the highly electronegative oxigen atom ,in each case the carbon bears a partial positive charge and the oxygen bears a partial.

However, S bearing functional groups of humic acids can quickly become saturated with Hg, therefore, most Hg^{2+} bound organic matter is found to be associated with O or N containing functional groups Gismera *et al.*, (2007). Because of such binding, the amount and type organic matter content in soil can significantly affect the solubility of mercury, mobility and, toxicity in soil Sysalova *et al.*, (2017). Chai *et al.* (2012) reported stable interactions between soil humic acids and mercury attributed to the abundance of O containing ligands. Humic acids have high complex stability potential, thereby, causing a decrease in the mobility of mercury Aijun *et al.*, (2006), whereas, mercury bound to fulvic acids increased a more labile form Wallschläger *et al.* (1998).

Liang *et al.* (2019) reported that kinetics of mercuric ion (Hg^{2+}) binding with heterogeneous naturally dissolved organic matter (DOM) has been hypothesized to result from competitive interactions among different organic ligands and functional groups of DOM for mercury (Hg^{2+}). However, an experimental protocol is lacking to determine mercury (Hg^{2+}) binding with various competitive ligands and DOM, their binding strengths, and their dynamic exchange reactions. In this study, a stepwise reduction approach using ascorbic acid (AA) and stannous tin [Sn (II)] was devised to differentiate Hg(II) species in the presence of two major functional groups in DOM: the carboxylate-bound Hg(II) is reducible by both AA and Sn (II), whereas the thiolate-bound Hg(II) is reducible only by Sn (II) Fig.(11).

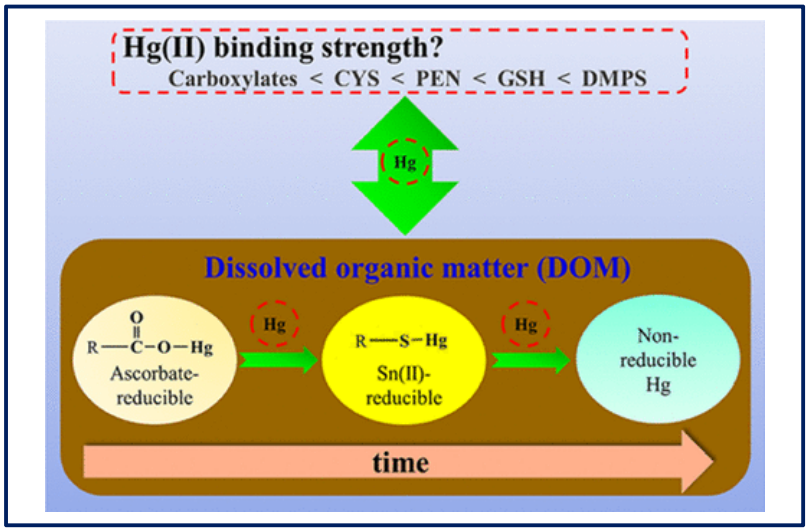

Fig. 11: Illustrates, a stepwise reduction approach using ascorbic acid (AA) and stannous tin [Sn (II)] was devised to differentiate Hg(II) species in the presence of two major functional groups in DOM. After: Liang *et al.* (2019).

Using this operational approach, the relative binding strength of mercury (Hg^{2+}) with selected organic ligands was found in the order dimer captopropane sulfonate (DMPS) > glutathione (GSH) > penicillamine (PEN) > cysteine (CYS) > ethylene diamine tetra acetate > citrate, acetate, and glycine at the ligand-to-Hg molar ratio < 2. Dynamic, competitive ligand exchanges for Hg^{2+} from weak carboxylate to strong thiolate functional groups were observed among these ligands and within DOM. This reaction depended on the relative binding strength and abundance of thiols and carboxylates, as well as reaction time. These results provide additional insights into dynamic exchange reactions of Hg^{2+} within multi compositional DOM in controlling the transformation and bioavailability of Hg (II) in natural aquatic environments.

The effect of soil organic matter on mercury sorption can also be influenced by human practices. Dai *et al.* (2013) considered mercury distribution of arable and natural unfarmed soils in the historic mercury mining area of Wanshan in Guizhou, China. It was stated that mercury was introduced to the study area via contaminated irrigation water, with mercury bound to particulate matter Fig. (12)

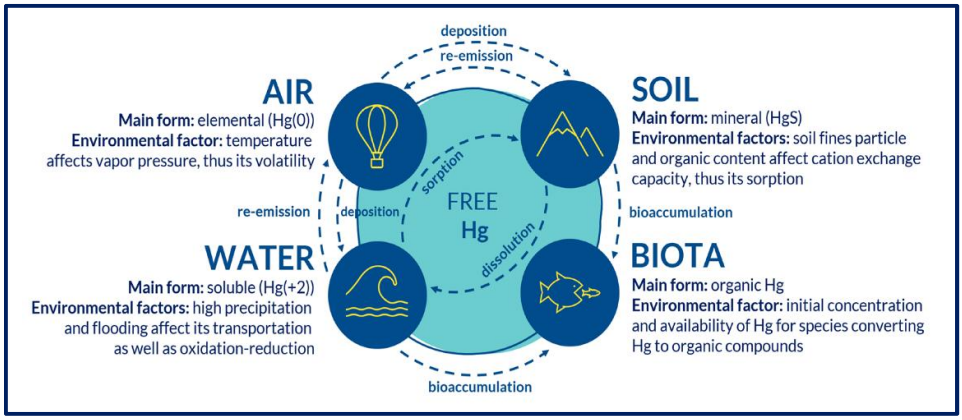

Fig. 12: Represents the main forms of Hg and environmental factors affecting Hg presence in different media. After: Guney *et al.* (2020).

Guney *et al.* (2020) stated that mercury is generally immobile in soils because of its extremely high affinity to organic matter and sulfur ligands O'Connor *et al.* (2019). Hence, elevated but immobile Hg concentrations are usually associated with soils with high organic content. However, Hg can be released into the atmosphere at high-temperature conditions Fig. (12) Neculita *et al.* (2005). It was also suggested that mostly immobile mercury fraction bonds to coarse-grain-sized soil particles, which only becomes mobile during the flooding period Eckle *et al.* (2020). Under anaerobic conditions, the microbial reduction of sulfates might take place in soils resulting in the formation of Hg sulfide (HgS, known as cinnabar), which is a chemically stable and highly insoluble form of Hg. Mercury adsorption also differs in soil types, and the highest sorption of low-mobility Hg is attributed to the finest size fraction, e.g., in clay, loams, and sands O'Connor *et al.* (2019). Mercury sorption is also attributed to the elevated specific surface area and cation exchange capacity in clays Guney *et al.* (2019). Water-soluble and highly mobile Hg fraction is significantly correlated with total organic carbon content in the soil, assuming that total organic carbon binds the mobile forms of mercury O'Connor *et al.* (2019). Farming cultivation practices generally decrease soil organic matter and increases air exposure. In the case of rice paddy soils, farming practices minimize exposure to air, and may reduce the fraction of large soil aggregates and increase soil organic matter content. Therefore, concentrations of mercury in rice paddy soils can significantly increase during long-term rice cultivation particularly, under a source of mercury Yin *et al.*, (2016).

4.1.2. Adsorption of mercury to soil matric

Reis *et al.* (2016) stated that adsorption of mercury on a soil matrix observed in two ways, either by non-specific or specific sorption. Cation exchange drives non-specific adsorption, resulting in outer-sphere complexes. The cation exchange process occurs rapidly and is considered reversible. In the case of specific adsorption, stable complexes are formed in which Hg diffuses inward to form inner-sphere complexes, considering slow non-reversible processes Bradl, (2004). Dissolution mechanism may cause mercury bound to soil matrices to become available. Dissolution may be brought about by the presence of complexing or chelating agents present in organic matter, for instance, produced by plant roots (exudates) or mycorrhiza. It is possible that dissolution will also occur due to reductive dissolution of Fe oxides. The effect of organic ligands on adsorption of mercury by mineral colloids in soils, in terms of the precise mechanisms and adsorption kinetics, remains somewhat unclear. Recently, Yang and Ok (2017) explored mercury adsorption by non-crystalline Al hydroxides under different pH conditions in the presence of selected organic ligands such as S containing cysteine, glycine, and citric acid. It was determined that mercury (Hg^{2+}) sorption by the control sample, cysteine and glycine systems was mediated by specific surface complexation, whereas, ligand exchange in the citric acid system was predominant. The mercury adsorption was observed to be initially rapid, and the amount of sorption decreased with increasing pH, except in the presence of higher concentrations of cysteine. Soil clay content has an important role in soil-Hg binding Biester *et al.*, (2002b), Boszke *et al.*, (2008). Rice paddy soils, which are characterized by their clayey as well as organic content, are susceptible to high Hg levels Yin *et al.*, (2016) Fig. (13).

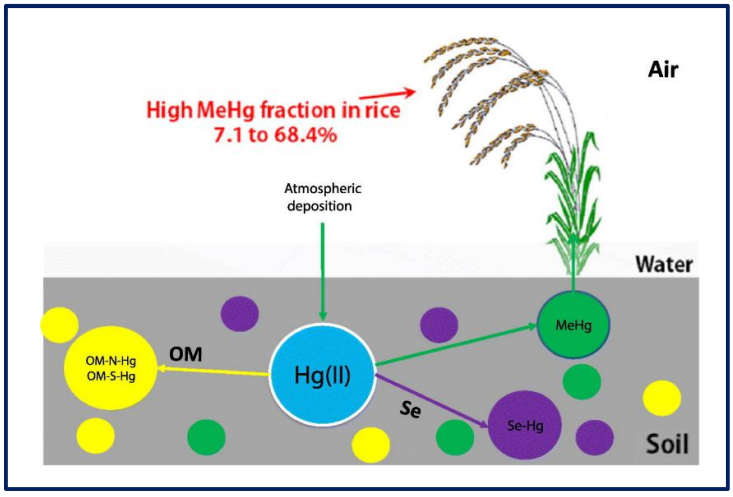

Fig. 13: Illustrates effects of soil prositiess on production and bioaccumulation of methylmercury in rice paddies at a mercury mining area

Adsorption capacity of clay to mercury can reach ~1000 mg for each 1cmol.kg^{-1} soil Antoniadis *et al.* (2017a), furthermore, increasing levels of mercury sorption on clay are associated with more clayey content in soil. Coufalík *et al.* (2012) noticed that high adsorption of mercury was correlated with the finest sized fraction and attributed to high specific surface area of clay fraction Coufalík *et al.*, (2012) and consequently, high cation exchange capacity (CEC) Fig. (14). Antoniadis *et al.* (2017a) stated that 2:1 clay such as illite have greater capacity to sorb Coufalík *et al.* (2012). The expandable clay minerals including smectites have greater capacity still Antoniadis *et al.*, (2017a

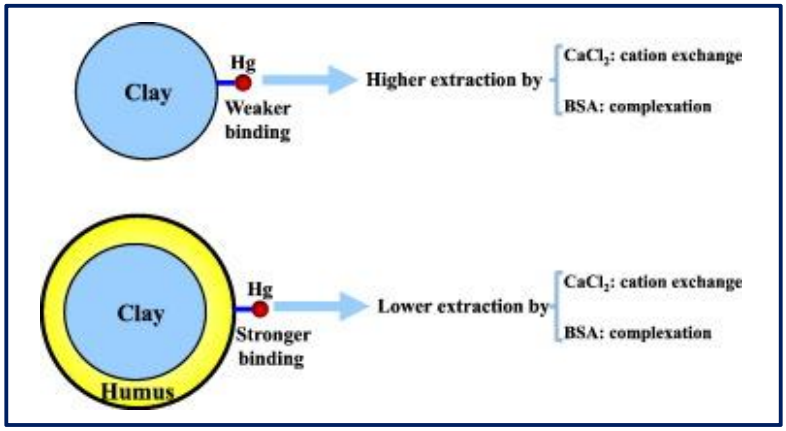

Fig. 14: Illustrates the potential bioavailability of mercury in humus- coated clay minerals.

Suggesting that adsorption of mercury (Hg) increased in clayey soils may also relate to binding with organic matter. Thermo desorption of Portuguese soils revealed a major peak at 125–250 °C ascribed to either $HgCl_2$, mercury bound to Fe oxides, or to humic substances Reis *et al.*, (2015a) and (2015b). This implies that the Hg in the sample may have been sorbed to the matrix mineral surfaces, or to organic matter. The precise species could not be distinguished by this technique. In fact, mercury (Hg) organic matter complexes can themselves be sorbed to soils matrix mineral surfaces - forming organ mineral Hg complexes thus simultaneously existing as different forms. In this case, it was reported that Fe oxides represented a large fraction of the soil (~10%), whereas, the organic matter content was low (~0.5%), and there were no suspected sources of chloride. Therefore, it was assumed that mercury (Hg) would likely be associated with Fe oxides. Thermo desorption analysis of weathered Amazonian soils by Do Valle *et al.* (2006) revealed peaks attributed to HgO release at ~150 °C and peaks at higher temperatures attributed to various mercuric salts. Biester and Scholz, (1997) mercury is released between 150 and 250 °C, the non-specific term matrix-bound Hg is often used. This is because desorption of Hg by mineral surfaces (e.g. Fe oxides).

5. Uptake, transport, and localization of Hg in plants

5.1. Absorption of mercury by plants

Plants can take up mercury through the roots architecture and accumulated in roots. Sierra *et al.* (2009) stated that some of mercury (Hg) absorbed remained in roots and then translocate to the aboveground and detected in leaves, flowers and other development tissues Fig. (15).

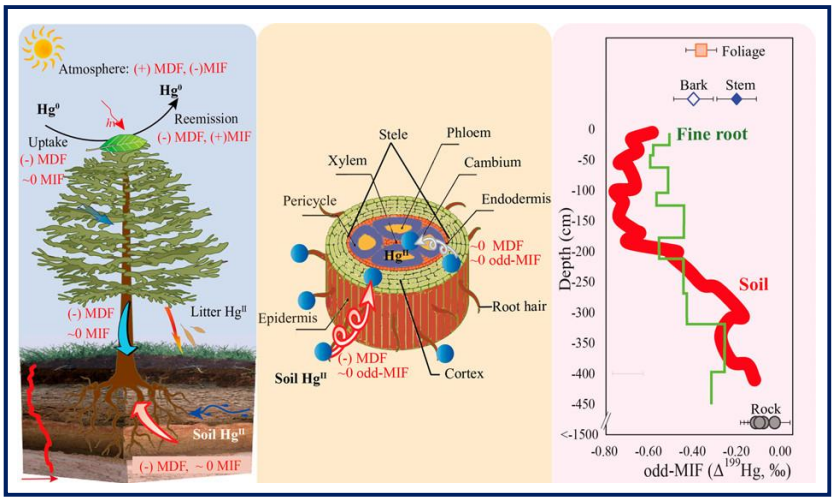

Fig. 15: Illustrates mercury uptake, accumulation and translocation in roots of forest, After: Yuan *et al.* (2022).

Yuan *et al.* (2022) stated that plant roots are responsible for transporting large quantities of nutrients in forest ecosystems and yet are frequently overlooked in global assessments of mercury (Hg) cycling budgets. We systematically determined the distribution of total mercury (Hg) mass and its stable isotopic signatures in a subtropical evergreen forest to elucidate sources of mercury Hg in plant root tissues and the associated translocation mechanisms. Mercury (Hg) stored in roots and its isotopic signatures showed significant correlations to those found in surrounding soil at various soil depths. The odd mass-independent fractionation (MIF) of root mercury (Hg) at a shallow soil depth displays a −0.10‰ to −0.50‰ negative transition compared to the values in aboveground woody biomass. The evidence suggests that root mercury (Hg) is predominantly derived from surrounding soil, rather than translocation of atmospheric uptake via aboveground tissues. The cortex has a more negative mass-dependent fractionation (MDF) of −0.10‰ to −1.20‰ compared to the soil samples, indicating a preferential uptake of lighter isotopes by roots. The similar MDF and odd-MIF signals found in root components imply limited Hg transport in roots. This work highlights that mercury (Hg) stored in plant roots is not a significant sink of atmospheric mercury (Hg). The heterogeneous distribution of mercury (Hg) mass in roots of various sizes represents a significant uncertainty of current estimates of mercury (Hg) pool size in forest ecosystems.

In white lupin, there is a short and long-term transport system for mercury (Hg^{+2}) uptake and translocation Esteban *et al.* (2008), suggesting there are transport systems for Hg influx to plant cells. Mercury (Hg^{+2}) import into root cells is possibly through Fe, Cu, or Zn transporters/channels Patra and Sharma (2000), Esteban *et al.* (2008). These transport systems usually have broad substrates Clemens (2006). Mercury (Hg^{+2}) uptake by plants is also affected by other factors in soils. For instance, the presence of arsenate significantly promoted the accumulation of mercury (Hg^{+2}) in the root of rice Du *et al.* (2005). Jing-Hua *et al.* (2014) reported that mercury (Hg^{+2}) uptake by seedlings of rice (*Oryza sativa* L.) grown in solution and interactions between Hg and arsenate uptake. The results showed that increasing (Hg^{+2}) concentrations in the nutrient solution decreased both root and shoot biomass. (Hg^{+2}) at 1.0 and 2.5 mg.L^{-1} caused 50% reduction in root biomass. A 50% reduction in shoot biomass occurred at (Hg^{+2}) concentrations of around 0.5 mg L^{-1}. Nevertheless, 0.5 mg As L^{-1} has no significant effect on plant yield. Hg accumulated in rice roots, and the Hg concentration factor in roots reached nearly 1900 at 2.5 mg .L^{-1}. The addition of arsenic (As) slightly increased the Hg concentration in the roots. However, arsenic (As) concentrations in the roots decreased significantly with increasing Hg concentration in the growth solution to 1.0 or 2.5 mg Hg L^{-1}. Shoot As concentrations decreased with increasing mercury (Hg^{+2}) concentrations in the growth solution, but increased again with further increase in Hg concentration to 2.5 mg L^{-1}. Possible mechanisms of (Hg^{+2}) uptake and interactions between mercury (Hg^{+2}) and arsenic (As) in the uptake process are discussed Fig. (16).

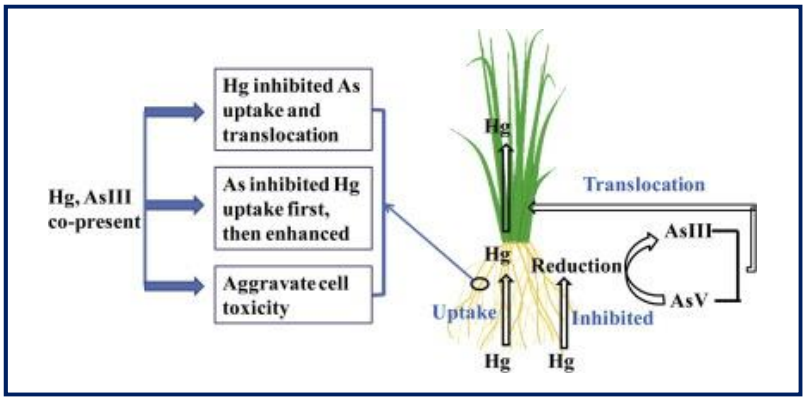

Fig. 16: Illustrates the interaction effects of mercury and arsenic on their uptake, association and toxicity in rice seedling, After: Jing-Hua *et al.* (2014)

Absorption and accumulation of Hg in rice plants has been conducted to study the IHg and MeHg accumulations in rice plant tissues during growth Zhang *et al.*, (2010); Meng *et al.*, (2012), (2014). While the rice plants were growing, the IHg concentration and accumulation both steadily increased in

the aboveground rice plant parts (e.g., leaves and stems) and increased considerably when the rice plants were exposed to high Hg vapor concentrations in the Hg mining areas, which may be related to the atmospheric Hg uptake pathway of the rice plants. Because atmospheric Hg is predominantly Hg0 (>95%) Schroeder and Munthes, (1998), the rice plant stomata is the potential pathway for atmospheric Hg0 to enter the aboveground rice plant parts (e.g., leaves and stems) through atmospheric exchange Assad *et al.*, (2016); Meng *et al.*, (2012). In addition, the atmospheric Hg0 vapor can be deposited on and adhere to the plant surface and subsequently be oxidized to Hg^{2+} Seigneur *et al.*, (1999), which then dissolves through the epidermis, passes into the subcutaneous cuticle, and eventually diffuses into the epidermal cells Moeckel *et al.*, (2008). Clearly, once the atmospheric IHg accumulates and fixes in the rice plant leaf and stem tissues, it usually cannot be re-emitted into the atmosphere or transferred to other rice plant tissue parts (e.g., seeds, husks, and roots) Meng *et al.*, (2012). However, the mechanism by which the atmospheric Hg speciation influences the IHg accumulation in the aboveground rice plant parts remains unclear. In contrast, the mechanism of Hg uptake in rice plant roots is clearer. The iron-containing gel film formed on rice plant root surface may be a barrier against IHg uptake and accumulation because the film effectively chelates IHg, thereby, blocking the Hg transfer pathway through the rice plant roots to the shoots Zhang *et al.*, (2010); Meng *et al.*, (2012). In addition, Hg–phytochelatin complexes form and effectively trap IHg in the rice plant roots but do not transfer the Hg to the aboveground tissues Krupp *et al.*, (2009). The plant availability and toxicity of the Hg both predominantly depend on the Hg chemical form. Meng *et al.* (2014) used X-ray absorption near-edge-structure spectroscopy (XANES) to study the Hg chemical forms in rice grains and found that the IHg was mainly bound to cysteine and phytochelatin, which may explain why most of the Hg was on the surface rather than the center of the grains (Rothenberg *et al.*, (2011). In fact, the immobilization of IHg in different rice plant tissues and accumulation of chelated IHg in the rice grains are the self-detoxification or -protection mechanisms of rice plants exposed to Hg pollution (Rothenberg *et al.*, (2011), (2012); Meng *et al.*, (2014). In rice plants, the MeHg accumulation process and mechanism are different from the IHg accumulation counterparts (Meng *et al.*, (2012), (2014). The MeHg bioaccumulation and transfer from the rice plant roots to the aboveground parts are believed to be dynamic. Rice plant roots can take up MeHg very efficiently from the soil media, indicating that at the plant–soil interface, MeHg is biosorbed more readily than IHg Krupp *et al.*, (2009), which may be related to the differences between the MeHg and IHg complexation. In rice plants, phytochelatins sequester IHg (e.g., Hg^{2+}) but not MeHg Krupp *et al.*, (2009). In addition, MeHg is believed to pass through the "iron plaque" physical barrier on the rice plant root surface, suggesting that MeHg acts as a mobile plant contaminant that can be more easily transferred to the aboveground plant tissues Zhang *et al.*, (2010) Fig.(17),(18).

Therefore, during the rice-growing season, the MeHg content is very limited in the rice plant roots. An additional study found that during rice plant growth, most of the MeHg was mainly stored in the leaves and stems of the early-maturing plants and that by harvest time, the MeHg temporarily stored in the leaves and stems was further transported to and accumulated in the mature rice grains Meng *et al.*, (2012). A relevant work wherein XANES was combined with high-performance liquid chromatography and inductively coupled plasma mass spectrometry (HPLC–ICP–MS) revealed that in the mature rice grains, the MeHg existed exclusively as MeHg–S compounds (e.g., MeHg–cysteine), which are mainly stored in grain protein and can thus effectively transfer across biological membranes following the migration of grain protein during rice growth (Meng *et al.*, (2014). Thus, free methylmercury–cysteine is a mobile complex that acts like free cysteine or amino acids and binds to the grain proteins. In the rice plant tissues, the dynamically changing MeHg chemical forms somewhat explain the mechanisms through which MeHg transfers and accumulates in rice (Meng *et al.*, (2014).

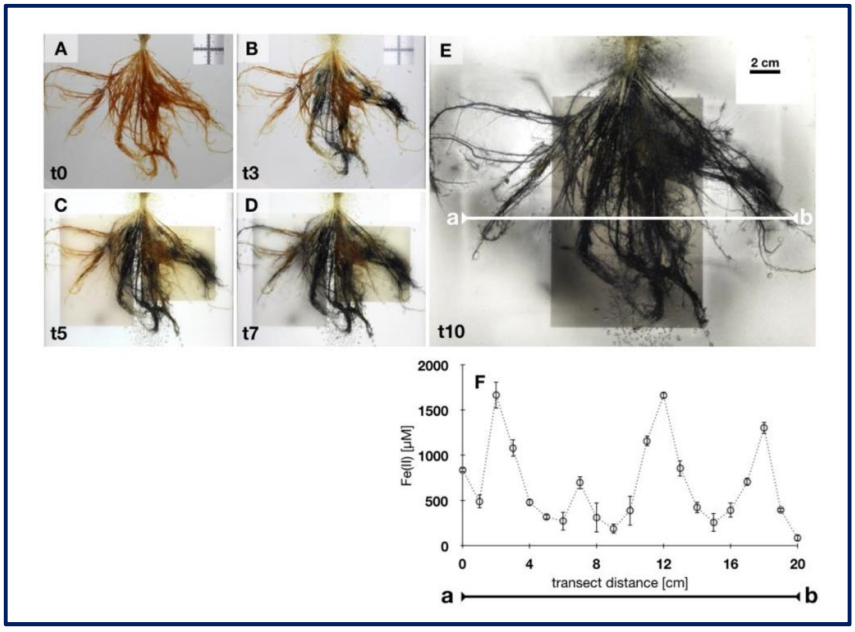

Fig. 17: Radial oxygen loss and iron geochemistry at the root–soil interface at the end of light incubated cycles: (A) Rice roots covered in iron plaque. (B) Radial oxygen concentrations surrounding root tips 35 DAT (DAT = days after transfer), a-b indicates a transect where O_2 and Fe(II) were measured and Fe(II) oxidation kinetics were calculated. (C) Transect a-b: representative concentrations of O_2, Fe(II) and calculated homogeneous Fe(II) oxidation rate along transect. After: Maisch *et al.* (2020)

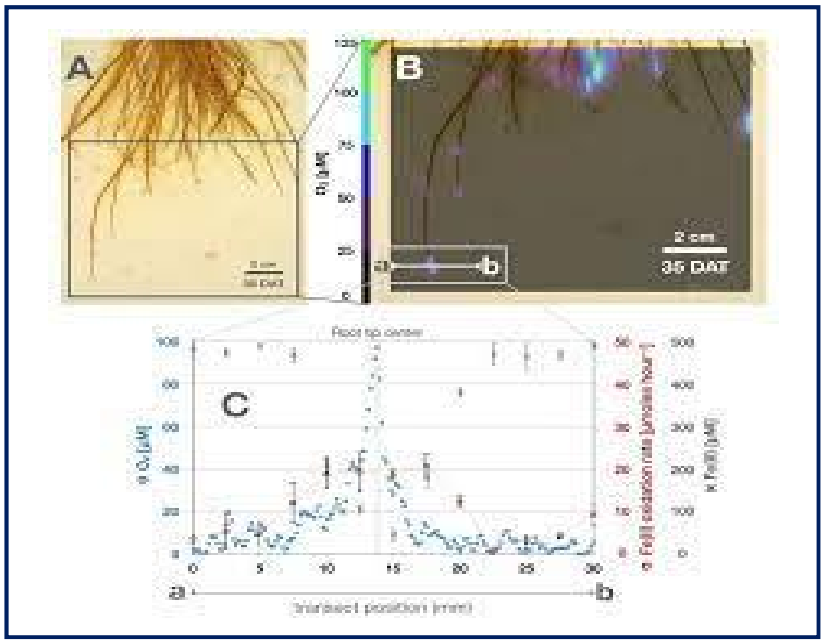

Fig. 18: Microbial Fe(III) iron plaque reduction. (A–E): Roots covered with iron plaque minerals incubated in rhizotron with a Fe(III)-reducing enrichment culture. Iron plaque minerals change in color over time A, t0: day 0–E, t10: day 10. (F): Voltammetric measurements along transect a-b in setup of figure, after 10 days of incubation, detect Fe(II) remobilized from root iron plaque is closely associated with roots. Error bars represent standard deviation from triplicate voltammograms. After: Maisch *et al.* (2020)

The absorption of arsenate increase the negative charge on root surface, enhance the adsorption of mercury Hg^{+2} on the root surface. Most of accumulated Hg^{+2}in plants remains in roots and only a small proportion can be translocate to shoots Wang (2004). Mercury Hg^{+2} trapped in roots, approximate 80 % of it is bound to cell wall wang and Greger (2004). This may be due to (**a**) Hg^{+2} ion is easy to interact with anionic compounds such as carbonate, sulfate, and phosphate forming the insoluble form through precipitates one , which limit symplastic mobility of Hg^{+2} and (**b**) Hg^{+2} ion bound to root cell walls has high cationic exchange capacity Chen *et al.* (2009b). For long distance transport of Hg^{+2} from roots to shoots, xylem-uploading process is indispensible. Some metal transports are active, whereas others are positive. Ever-increasing population places great importance on the availability of sufficient food sources, resulting in an increased demand for global food production to fulfill the needs of the growing population, leading to various facades of environmental pollution. Of the various pollutants contributing to the damage to the environment, heavy metals are well recognized, particularly, due to their persistence in the environment, toxicity, and bio-accumulative nature, leading to unfavorable repercussions on human health and the ecosystem. Furthermore, heavy metals originate from weathering of metal-bearing rocks, volcanic eruptions, and atmospheric depositions, anthropogenic activities including mining, leakage and emissions from industries, use of agrochemicals including fertilizers, and application of sewage sludge to croplands are the key sources of heavy metal accumulation in soil and water ecosystems. Heavy metal accumulation can further be defined as an amalgamation of heavy metal elements to the ecosystem, particularly to the aquatic ecosystem. Rice and an array of aquatic plants such as water chestnut (*Trapa spp*.), water spinach (*Ipomoea aquatica*), watercress (*Nasturtium officinale*), taro (*Colocasia esculenta*), and lotus (*Nelumbo nucifera*) are important sources of food, particularly, in many Asian countries as well as in west and central African regions. These plants accumulate heavy metals causing various issues to human health, the environment, and ecosystems Fig. (19).

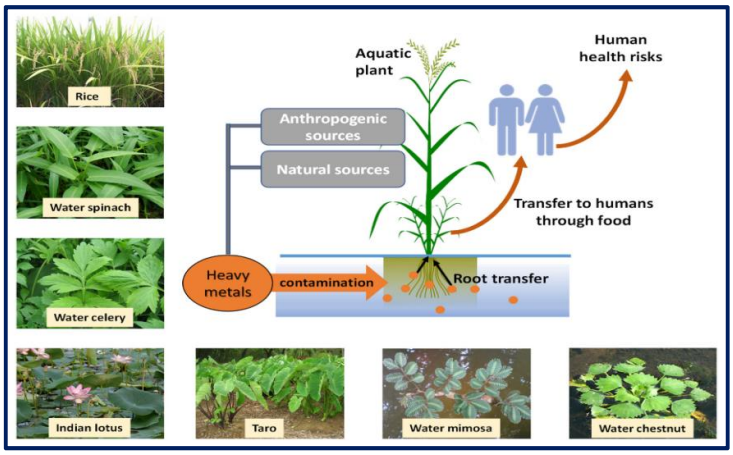

Fig. 19: Illustrates the pathway of heavy metal transfer from original sources to humans. Some common aquatic plants used for human food is inset in the image. After: Mohammad *et al.* (2021)

Mohammad *et al* (2021), found that aquatic ecosystems are contaminated with heavy metals by natural and anthropogenic sources. Whilst some heavy metals are necessary for plants as micronutrients, others can be toxic to plants and humans even in trace concentrations. Among heavy metals, cadmium (Cd), arsenic (As), chromium (Cr), lead (Pb), and mercury (Hg) cause significant damage to aquatic ecosystems and can invariably affect human health. Rice, a staple diet of many nations, and other aquatic plants used as vegetables in many countries, can bioaccumulation heavy metals when they grow in contaminated aquatic environments. These metals can enter the human body through food chains, and the presence of heavy metals in food can lead to numerous human health consequences. Heavy metals in aquatic plants can affect plant physicochemical functions, growth, and crop yield. Various mitigation strategies are being continuously explored to avoid heavy metals entering aquatic ecosystems. They also reported that with their origin in various natural and anthropogenic sources,

heavy metals might contaminate aquatic ecosystems. Use of contaminated water for irrigation of crops can allow direct transport of heavy metals into plants. Aquatic plants can absorb heavy metals through the root systems that transport the metals to edible plant parts, such as leaves, flowers, corms, stems, seeds, etc., with subsequent introduction into the food chain, as confirmed by various reports. Direct ingestion of heavy metal-contaminated aquatic plants and their bioaccumulation in food chains are the main sources of human exposure to toxic heavy metals from aquatic food plants. This exposure can lead to various chronic and acute diseases and health consequences, such as kidney damage. Whilst plants use many heavy metals as micronutrients in low concentrations to fulfill their nutritional and physiological needs, some heavy metals can be phytotoxic, leading to disruptions of developmental and metabolic processes, including the plant's physiology, photosynthesis, morphology, cell structure, and nutrient balance. These disruptions can lead to decreased growth and yield of food crops as well as ecological imbalance. Progress has been made in phytoremediation of contaminated water bodies, Nano technological advances for the removal of heavy metals, and genetic modification of plants to tolerate higher levels of accumulated heavy metals

In addition to Hg uptake from roots, the aerial part of plants, particularly, leaf is another important way for accumulation of Hg Ericksen and Gustin (2004); Ericksen *et al.* (2003); Millhollen *et al.* (2006a); Fay and Gustin (2007), due to the industrial emission of Hg to the air and microorganism-mediated Hg emission from soils Lindberg *et al.* (2007). In a field study, the above ground tissues of maize and wheat were exposed to an open top chamber filled with Hg contaminated air for an entire growing season; Hg concentrations in foliage's were closely correlated to the air but not related to the soil Hg concentrations, indicating that the air Hg was the major source of Hg accumulated in crop foliage's Niu *et al.* (2011). Linear correlations (R2 = 0.64–0.98) between foliar Hg concentrations and air Hg concentrations have been established in ryegrass and leafy vegetables De Temmerman *et al.* (2007), De Temmerman *et al.* (2009).

Zhou *et al.* (2021) reported that mercury (Hg) contamination from urban and industrial, mining or smelting sites, natural Hg enrichments exist on the global mercuriferous belts found along Earth plate margins, leading to large-scale Hg mineralization zones: Circum-Pacific, Mediterranean, Central Asia and Mid-Atlantic ridges, with many Hg mines distributed along these zones Liu *et al.* (2020). When exposed to high soil and atmospheric Hg levels, plant growth can be decreased due to Hg toxicity Anjum *et al.* (2015), Pogrzeba *et al*. (2019). However, most plants grow normally under lightly to moderately polluted areas, but will show substantial Hg enrichments in their tissues.

In comparison with remote, non-enriched sites, median Hg concentrations of vegetation from Hg-enriched areas in our database show significantly higher Hg concentrations ($P<0.01$) by factors of 1.2–5.7 across all tissues. Specific tissue responses are dependent on the type of exposure, with soil Hg contamination resulting largely in elevated root Hg concentrations, while not significantly affecting aboveground tissue concentrations. In turn, atmospheric Hg contamination significantly elevates Hg levels in aboveground Hg concentrations ($P<0.01$) but did not affect belowground tissues. The potential use of plant Hg uptake has received interest as an alternative method for traditional physico-chemical methods of remediation of Hg-enriched sites, termed phytoremediation. In summary, there are three main approaches of Hg phytoremediation: phytostabilization, phytovolatilization and phytoextraction. Phytostabilization immobilizes Hg in soil through biochemical processes, either via Hg accumulation in roots or chelating Hg in the root zone. Candidate plants used for phytostabilization have extensive root systems, are tolerant to Hg toxicity and are adaptive to site-specific environments Anjum *et al.* (2015 Pogrzeba, M. *et al.* (2019) Phytovolatilization refers to the uptake of elements by plant roots, translocation through the xylem and subsequent emission to the atmosphere Wang *et al.* (2012). Phytovolatilization is unique to Hg owing to its relatively high volatility; however, there are few studies on phytovolatilization of Hg via vegetation, in part, because of its inefficiency (<0.98% remediation) Moreno *et al.* (2005), difficulties in monitoring volatilization fluxes and possibly related to concern over secondary contamination by emitting Hg to the atmosphere.

Instead, most studies on phytoremediation have focused on phytoextraction, whereby Hg is removed from soil by harvesting vegetation that has taken up Hg from soils. No plant has been identified as a Hg hyperaccumulator, which are plants that are capable of growing under high contamination and take up metals via roots and bio concentrate them in their shoots Rascio, and Navari-Izzo, (2011). Vegetation known to show a potential to bio accumulate Hg have been shown to remove less than 0.2% of the Hg in Hg-enriched soils, even when chemically assisted Wang *et al.* (2011),(2018). Hence, in contrast to

some other toxic trace metals where phytoextraction is highly efficient (such as 32.4–84.5% removal of soil cadmium by *Sedum plum* bizincicola) Fan *et al.* (2019), phytoextraction is considered of low efficiency for Hg. Adsorption processes Arnold *et al.* (2018), Chiarantini *et al.*(2016) Across the bark, Hg concentrations markedly decrease from the outermost to the innermost layers (including the phloem) Zhou *et al.* (2016) indicating little transport through the bark. Potential pathways for Hg in bole wood include root uptake and translocation through the xylem, foliage uptake and translocation by phloem transport, and transfer from the bark Fig. (20). However, Hg uptake to bole wood, which is the tissue showing by far the lowest Hg concentrations is considered to be dominated by translocation of foliage Hg to tree rings through phloem transport, whereas transport through translocation from roots and bark is likely negligible Arnold *et al.* (2018), Greger *et al.* (2005).

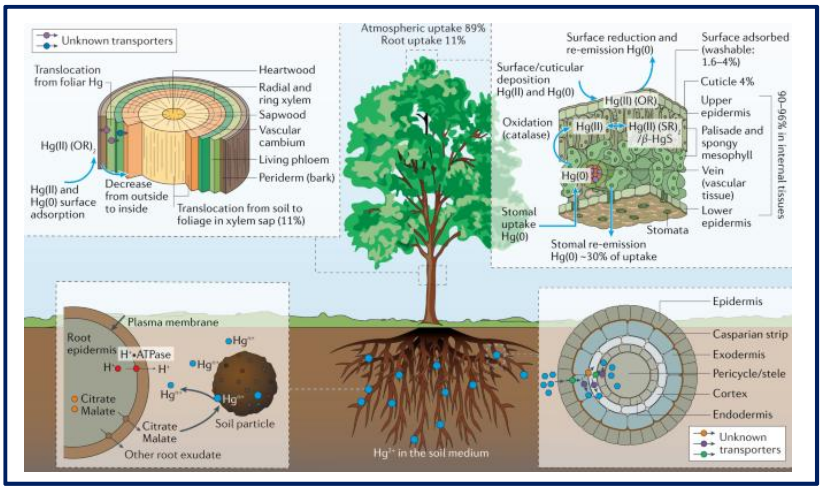

Fig. 20: Illustrates the pathways of plant Hg uptake. Plants uptake atmospheric mercury (Hg) through their foliage via stomatal and cuticular uptake, and transport Hg through leaf tissues and translocate Hg via phloem transport to woody tissues. Plants also uptake Hg from the soil through their roots, with little transport of Hg through root tissues into xylem. Finally, there is passive uptake of atmospheric Hg to bark. After: Vorholt (2012) and Zhou *et al.* (2021)

Notably, this transport could enable the use of tree ring Hg to track historic, local, regional and global Hg exposures Arnold, et al. (2018), Peckham *et al.* (2019), Zhou *et al.* (2016), Hojdova *et al.* (2011). Below ground, plant roots and excretions (chelators) can induce pH variations and redox reactions in soils, which, subsequently, lead to cation exchange of divalent Hg and solubilization of Hg from nearly insoluble soil Hg precipitates Tangahu *et al.* (2011), Farella *et al.* (2006). Mercury then likely penetrates into root cells as a hitchhiker using transporters for other elements Clemens (2006), Clemens, and Ma (2016) as Hg is a non-essential element. Absorbed Hg is largely restricted to the cell walls of the outer layers of the root cortical cylinder, as well as to the central cylinder and parenchyma cell nuclei Cavallini *et al.* (1999). Accumulation in root cells can reduce the movement of Hg from the root into the xylem, and transport of Hg–phytochelatin complexes into vacuoles can restrict phloem mobility Clemens (2006), Clemens and Ma (2016). Low Hg translocation from soils to aboveground tissues has been attributed to effective Hg retention in roots Wang *et al.* (2012). However, no specific transport molecules involved in Hg uptake by roots and translocation in roots are known.

Root Hg concentrations have been shown to linearly correlate with soil concentrations Niu *et al.* (2011), Niu *et al.*(2013), Zhou *et al.* (2015) and show low sensitivity to air Hg concentrations14, leading to the view that Hg in roots is derived primarily from soil uptake. However, exceptions have been reported in quaking aspen Frescholtz *et al.* (2003) and wheat Niu *et al.* (2011), Millhollen *et al.* (2006) under very high atmospheric Hg exposures (20–40 times ambient air concentrations). Moreover, stable Hg isotope studies have pointed to contrasting Hg origins in roots. For example, rice plants grown in contaminated soils showed root Hg with the same isotopic signature as the surrounding Soil Yin *et al.* (2013), indicating root uptake. In contrast, substantial foliage-to-root Hg transport was observed in

a forest, where atmospheric Hg (0) uptake via foliage accounted for 44–83% of Hg in tree roots Wang *et al.* (2020). In the latter study, large roots showed somewhat higher proportions of atmospheric Hg (0) compared with small roots (59% versus 64%) Wang *et al.* (2020), possibly related to lower surface areas and reduced absorptive potential of large roots Wang *et al.* (2012), Rewald *et al.* (2011). The role of atmospheric uptake in root Hg merits further detailed investigations, as this phenomenon would substantially increase estimates of plant Hg uptake from the atmosphere due to high turnover rates of roots, which could equal that of leaf litter fall Wang *et al.* (2012).

Non-vascular vegetation, including lichens and mosses (slow-growing cryptogamic organisms without root systems or thick waxy cuticles), generally, show much higher Hg concentrations compared with vascular plants. Mercury bioaccumulation in mosses and lichens is controlled by numerous biotic and abiotic factors, including: species, whereby different moss and lichen species show large differences in Hg concentrations under the same exposures Balabanova *et al.* (2017), Solberg and Selmerolsen (1978); substrate and local soil Stankovic *et al.* (2018), Salemaa *et al.* (2004); growth rate and surface area Lodenius (1998), Bargagli (2016); exposure to pollution source49; temporal variation Zechmeister *et al.* (2003); and chemical composition of wet and dry deposition Wolterbeek and Bode (1995), Wolterbeek *et al.* (2003). Metals accumulate in mosses and lichens through intracellular and extracellular processes, as a lack of thick waxy cuticles in lichens and mosses allows cations to diffuse readily through cell walls Dolegowska and Migaszewski (2015). In the extracellular process, metals are intercepted and adsorbed and/or absorbed by exchange sites outside of cell walls and plasma membrane surface. In the intracellular process, Hg is subsequently trapped as particles on the cell surface layer or translocated inside the cell Stankovic *et al.* (2018), Tyler (1990), Wang *et al.* (2019). In addition to surface deposition of oxidized atmospheric Hg (reactive gaseous Hg and particulate-bound Hg), Hg(0) assimilation could contribute to trapping and sequestering Hg in moss and lichen tissue, but the specific methods of uptake, binding and accumulation from the atmosphere are unknown. After uptake, Hg (0) is oxidized to Hg (II) and subsequently immobilized in moss and lichens for 4–5 weeks Lodenius *et al.* (2003), Bargagli (2016), Vannini *et al.* (2014). Lichens show significantly higher Hg concentrations (78 μg kg−1 [10–180 μg kg−1]) than mosses (51μgkg−1 [2–165μgkg−1]) in our data set ($P<0.05$). This difference is likely related to the different morpho-physiological properties and abilities to intercept airborne particles of lichens and mosses Bargagli (2016), as lichens often accumulate higher contents of atmosphile elements (derived from atmospheric sources), whereas mosses have shown higher contents of lithophile elements, such as dust, Adamo *et al.* (2008), Bargagli (1995). Staple isotope analyses indicate that atmospheric Hg (0) accounts for 76% and 86% in ground and tree mosses, with the remaining 24% and 14% originating from Hg (II) contribution Wang et al (2020). Hence, where lichens and mosses represent a significant component of plant communities, such as in the Arctic tundra, their high tissue concentrations are responsible for high atmospheric deposition loads via uptake of atmospheric Hg exceeding Hg deposition by vascular plants Obrist et al (2017), Olson *et al.* (2019). Furthermore, Hg concentrations in mosses and lichens can maintain a state of dynamic equilibrium with atmospheric Hg concentrations Nieboer and Richardson (1979), Walther *et al.*(1990), and lichens and mosses increase Hg(0) uptake from the atmosphere when exposure is high Pradhan *et al.* (2017). Passive Biomonitoring using lichens and mosses for atmospheric Hg could, hence, be cost-effective and benefit from abundant distribution, structural simplicity, rapid growth rate and ease of sampling Dolegowska and Migaszewski (2015), Wang *et al.* (2019), Garty (2001), but this application has shown limited success. For example, there were weak correlations between atmospheric Hg deposition and Hg accumulation in moss and soils across large south-to-north gradients in Norway Nickel *et al.* (2017). In contrast, there was a lack of correlation between modelled atmospheric Hg deposition and moss concentrations across a large network of sites in Europe, and moss collected in Norway showed no distinct north-to-south patterns, in spite of expected gradients in atmospheric Hg pollution Harmens, *et al.* (2010). Bargagli *et al.* (2016), Dolegowska and Migaszewski (2015), concluded that Hg concentrations in lichens and mosses are impacted by many environmental variables, which complicates its use as a biomonitor for atmospheric Hg concentrations and deposition. High concentrations of Hg in bottom leaves of *Rudbeckia hirta* were attributed to the Hg emission from soils Millhollen *et al.* (2006a, b). Hg exchange between foliar and surrounding air is a dynamic process. The net deposition rates of Hg on leaves increased with the atmospheric Hg concentrations Ericksen and Gustin (2004). The mechanisms of how Hg enters into leaves remains elusive, but stomata may be responsible for the uptake of atmosphere Hg by leaves through gas exchange.

6. Mercury concentration in plant

Vegetation affects environmental factors at the ground surface by reducing solar radiation, temperature, and wind velocity and serves as a surface for Hg uptake Zhu *et al.* (2016). Many studies have recognized the essential role of terrestrial plants in the biogeochemical cycling of Hg Gustin *et al.* (2004); Fantozzi *et al.* (2013); Mazur *et al.* (2014) Fig. (21). Bishop *et al.* (2020) reported that recent advances in terrestrial mercury cycling, terrestrial mercury (Hg) research has matured in some areas, and is developing rapidly in others. Summarizing the state of the science circa 2010 as a starting point, and then present the advances during the last decade in three areas: land use, sulfate deposition, and climate change. The advances are presented in the framework of three Hg "gateways" to the terrestrial environment: inputs from the atmosphere, uptake in food, and run off with surface water. Among the most notable advances: **(a)** the Arctic has emerged as a hotbed of Hg cycling, with high stream fluxes and large stores of Hg poised for release from permafrost with rapid high-latitude warming. **(b)** the bi-directional exchange of Hg between the atmosphere and terrestrial surfaces is better understood, thanks largely to interpretation from Hg isotopes; the latest estimates place land surface Hg re-emission lower than previously thought. **(c)** artisanal gold mining is now thought responsible for over half the global stream flux of Hg. **(d)** there is evidence that decreasing inputs of Hg to ecosystems may bring recovery sooner than expected, despite large ecosystem stores of legacy Hg.

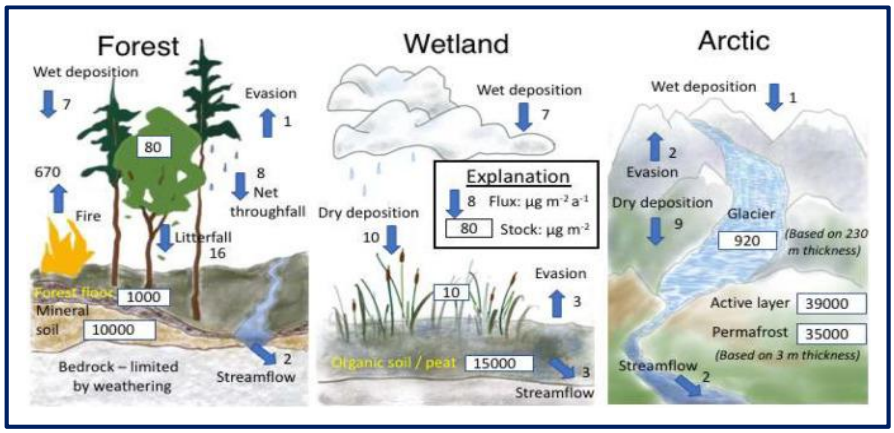

Fig. 21: Typical values for stocks and annual fluxes for THg in the northern temperate/boreal forest and wetland landscapes, and the Arctic landscape. The intent is to show relative magnitudes; actual values and even net flux directions may vary widely among ecosystems, and have high uncertainty. Belowground Hg stocks may consider different depths. Values are specific to that land cover or process. In the case of fire, the value is for a one-time release (not per year); the value is high because it is specific to burned area. Forest and Wetland panels are modified from Shanley and Bishop (2012). Arctic panel values are calculated from data of Schuster *et al.* (2002), Schuster *et al.* (2018), Obrist *et al.* (2017), Sonke *et al.* (2018), and Bishop *et al.* (2020)

Approximately 80% of total Hg accumulated in the aboveground biomass was found in the leaves, and approximately 1% of that Hg is methylated. The concentrations of Hg in aspen tissue grown in high-Hg soil increases in the following order: Stems<branches<petioles<roots<leaves Ericksen *et al.* (2003). Research conducted by Leonard *et al.* (1998) in Nevada (USA) in an area with high levels of Hg contamination revealed that for the plant species *Lepidium latifolium*, 70% of the Hg taken up by the roots during the growing season was emitted to the atmosphere. The main source of Hg in leaves comes from air pollution with Hg0 and not from soil contamination Gustin *et al.* (2004), Frescholtz *et al.* (2003), Assad *et al.* (2016). The studies by Fleck *et al.* (1999) of *Pinus resinosa* have shown that neither woody tissue Hg nor any amount of Hg in the soil or forest floor were closely related to foliar levels, while for some relationships, the opposite was true. The authors interpret these data as indicating that Hg in plant tissues is derived directly from the atmosphere and not from the soil. It is estimated that in highly contaminated soils, generally, less than 2% of the Hg present is available for plants Dago *et al.* (2014). Total leaf concentrations of Hg varied among species and were most closely correlated with

the number of stomates per sample, thus, supporting the hypothesis that stomatal uptake of atmospheric Hg (most likely Hg0) is a potential uptake pathway Laacouri *et al.* (2013). Research by Arnold *et al.* (2018) also indicated the importance of the nonstomatal pathway for the uptake of total gaseous Hg (TGM). Plants growing beyond the influence of high Hg emissions contained less than 100 ng g^{-1} .T Hg. Plants growing approximately factories are large emitters of Hg, such as those around Hg mining sites Moreno-Jiménez *et al.* (2006), Qian *et al.* (2018) and chlor-alkali mining sites De Temmerman etal. (2009). Au mining sites Egler *et al.* (2006), Svoboda *et al.* (2006) may also contain extremely high Hg contents. Mushrooms have been identified as organisms that accumulate more Hg than other plants Falandysz *et al.* (2018). A synthesis of published vegetation Hg data from the western United States showed that aboveground biomass concentrations followed the order: Leaves (26μg.kg^{-1})~branches (26 μg.kg−1)>bark (16 μg. kg^{-1})>bole wood (1 μg. kg^{-1}) Obrist *et al.* (2016) . Mercury concentrations in leaves were monitored from the emergence to senescence and showed a strong positive correlation with leaf age Assad *et al.* (2016), Laacouri *et al.* (2013), Millhollen *et al.* (2006).

Mercury does not have any beneficial effects on organisms and is thus, regarded as the "main threat" since it is very harmful to both plants and animals; pollutes the air, water and soil; and is toxic Asati *et al.* (2016). Mercury has toxic effects on plants, even at low concentrations, and leads to growth retardation Ahammad *et al.* (2018) and many other adverse effects Shahid *et al.* (2020). Mercury in plants is strongly bound to sulfhydryl/thiol groups of proteins and forms SHgS. Mercury toxicity in plants occurs via its binding to SH groups of proteins, displacement of essential elements and disruption of the protein structure Safari *et al.* (2019) . This biochemical property probably determines the toxic effects on plants Kabata-Pendias and Pendias (2001), Zhou *et al.* (2008), Azevedo and Rodriguez (2012). Studies of the toxic effects of Hg on soil organisms and native plants in fields are limited. The effects of Hg are usually examined in sterile and much-simplified laboratory conditions, which may differ from field conditions to varying degrees Patra and Sharma (2000). The field study of Moreno-Jiménez *et al.* (2006) was conducted in the mining district of Almadén (Spain), which is a cinnabar (HgS) enriched zone, from which one-third of the total Hg produced worldwide is extracted. Mining activity began more than 2000 years ago, and Hg has influenced no other region in the world for such a long period. The region is considered one of the regions most polluted by Hg in the world. Mercury concentrations in the field plants *Rumex induratus* and Marrubium vulgare grown in these soils can be considered phytotoxic, although no symptoms of Hg toxicity have been observed in any of the studied plant species. In most contaminated soils and mine tailings, Hg is not readily available for plant uptake Moreno *et al.* (2004). The absorption of organic and inorganic Hg from soil by plants is low, and there is a barrier to Hg translocation from plant roots to tops. Thus, large increases in soil Hg levels produce only modest increases in plant Hg levels by direct uptake from soil Patra and Sharma (2000). In terrestrial vegetation, Hg in the aboveground biomass originates primarily from the atmosphere, whereas, Hg in the roots comes from the soil Selin *et al.* (2007), Obrist (2007).The research conducted by Lomonte *et al.* (2010) suggested the existence of Hg stress-activated defense mechanisms in plants and hypothesized that these mechanisms were likely the reason for the increased production of sulfur compounds in the tested plant species, which stimulated their growth. Mercury has very limited solubility in soil, low availability for plant uptake and no known biological function, which may explain why Hg-hyperaccumulating plants have not yet been identified, meaning that a method for Hg phytoremediation in soils contaminated with Hg has not yet been developed Lomonte *et al.* (2010). However, studies suggesting the use of transgenic plants for phytoremediation have been published recently Fasani *et al.* (2018), Ahmed *et al.* (2019).

The significant toxic effect of Hg on plants is the generation of reactive oxygen species (ROS) Kim *et al.* (2017), e.g., superoxide anion radicals, H_2O_2, and hydroxyl radicals (OH.) Cho and Park (2000), Israr and Sahi (2006). Detoxification mechanisms to combat Hg. Induced oxidative stress include enzymatic antioxidants and some nonenzymatic antioxidants, such as the following: glutathione Zhang *et al.* (2017) , phytochelatin Gómez-Jacinto *et al.* (2015) , salicylic acids Wani *et al.* (2017) , ascorbic acid Kováčik *et al.* (2017) selenium, Zhou *et al.* (2017) , proline Seneviratne *et al.* (2019) and tocopherols, Hasanuzzaman *et al.* (2012) Fig.(22) .

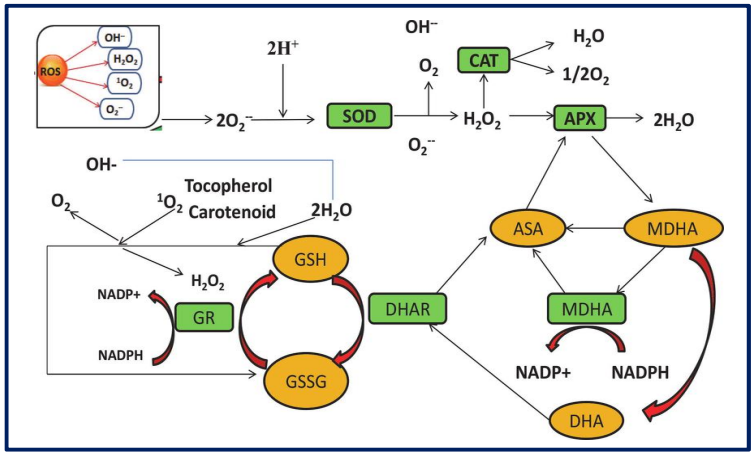

Fig. 22: Illustrates the enzymatic and non-enzymatic antioxidant mechanism to defend oxidative stress enzymatic and nonenzymatic antioxidants in algae.ASC (Ascorbate),APX, (Ascorbate peroxidase), CAT Catalase, DHA (Dehydroascorbate), GSH (Glutathione), GR (Glutathione reductase) , GSSG (Glutathione disulfide),MDHA (Monodehydroascorbate),SOD (Superoxide dismutase),DHA (Dehydroascorbate).After Kumari *et al.* (2022)

Kumari *et al.* (2022) stated that plants respond to various stresses during their lifecycle among which abiotic stress is the most severe one comprising heat, cold, drought, salinity, flooding, etc. which take a heavy toll on crop yield worldwide in every corresponding year. ROS has a dual role in abiotic stress mechanisms where, at high levels, they are toxic to cells while at the same time, the same molecule can function as a signal transducer that activates a local as well as a systemic plant defense response against stress. The most common ROS species are hydrogen peroxide (H_2O_2), superoxide anions (O^{-2}), hydroxyl radicals (OH^-), and singlet oxygen ($1O^{-2}$) which are results of physiological metabolism often controlled by enzymatic and non-enzymatic antioxidant defense systems. ROS generally, accumulate in plants during abiotic and biotic stress conditions resulting in oxidative damage that ultimately leads to programmed cell death. Many ROS scavenging pathways have been well studied against stress responses. Through careful manipulation of ROS levels in plants, we can enhance stress tolerance in plants under unfavorable environmental conditions. This process is correlated with the disruption of bio membrane lipids and cellular metabolism, resulting in plant injury Cargnelutti *et al.* (2006). Increasing levels of mercury species in the soil exert a wide range of adverse effects on the growth and metabolism of plants Asati *et al.*, (2016), Patra *et al.* (2004), Nagajyoti *et al.*, (2010), such as reduced photosynthesis, transpiration, water uptake, chlorophyll synthesis.

Sapre *et al.* (2019) reported that organic form of mercury severely affects plants, as they are more toxic than inorganic (Hg^{2+}) counter parts Patra and Sharma (2000). Mercury has its toxic effect on most of the crop species, beyond the tolerance limit. It tends to amass in the roots; hence, the phytotoxic symptoms are also noticed in roots Chen *et al.* (2014). The excess mercury in the soil is taken up by plants, causing disturbance and malfunction to many of the biological processes, including photosynthesis, respiration, transpiration and cell division Fig. (23).

The plausible mechanism of mercury toxicity is its ability to react with the sulfhydryl (SH) groups of proteins and enzymes; similarly, it has high affinity for the phosphate groups of lipids, energy-rich molecules like ATPs and nucleotides. It is also noted that it also substitutes the essential ions such as Mg^{2+} ion in chlorophyll Azevedo and Rodriguez (2012). Mercury also messes up with the aqua-porins (water channels), causing impaired transpiration and subsequent water uptake via vascular tissues Zhou *et al.* (2008) Fig. (24).

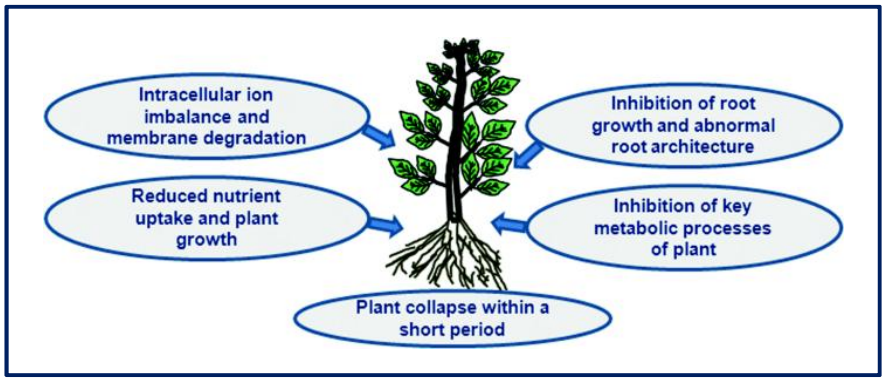

Fig. 23: Illustrates the effects of mercury toxicity on plants. After: Sapre *et al.* (2019)

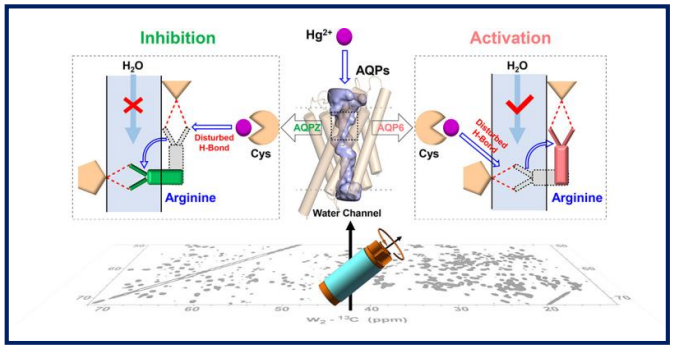

Fig. 24: Aquaporins are inhibited by mercury ions. After: Xie *et al.* (2022)

Xie *et al.* (2022) noted that aquaporins are transmembrane channels that allow for the passive permeation of water and other small molecules across biological membranes. Their channel activities are sensitive to mercury ions. Intriguingly, while most aquaporins are inhibited by mercury ions, several aquaporins are activated by mercury ions. The molecular basis of the opposing aquaporin regulation by mercury remains poorly understood. Herein, we investigated AqpZ inhibition and AQP6 activation upon binding of mercury ions using solid-state NMR (ssNMR) and molecular dynamics (MD) simulations. Based on the structure of the Hg–AqpZ complex constructed by MD simulations and ssNMR, we identified that the pore closure was caused by mercury-induced conformational changes of the key residue R189 in the selectivity filter region, while pore opening was caused by conformational changes of residues H181 and R196 in the selectivity filter region in AQP6. Both conformational changes were caused by the disruption of the H-bond network of R189/R196 by mercury. The molecular details provided a structural basis for mercury-mediated functional changes in aquaporins.

It deliberately disrupts the plant antioxidant defense enzymes, especially glutathione reductase (GR), superoxide dismutase (SOD), catalase and ascorbate peroxidase (APX). Besides, it also affects the other antioxidant entities such as glutathione (GSH) and non-protein thiols Israr *et al.* (2006), Zhou *et al.* (2008). The plants can tolerate the effect of mercury toxicity to some extent by the interplay of various physiological and molecular mechanisms. First, when plants come into contact with mercury ions, they prohibit or reduce the uptake of mercury into the roots by either complexing them to cell wall or root exudates; if it enters the root cell, the metal ion is restricted to the apoplasts. Nevertheless, if still the mercury ions gain entry into the plant cell, they are countered by detoxification through compartmentalization into vacuoles or complexation with amino acids, organic acids, chelation by phytochelatins (PC) and metallothioneins (MT). Further, some non-enzyme antioxidants such as a-tocopherol and GSH also aid in combating mercury toxicity Kalaivanan and Ganeshamurthy (2016). These processes mostly put a check on translocation of mercury ions to the leaf tissues and thereby shielding the photosynthesis from detrimental effect of mercury Rascio and Navari-Izzo (2011). Finally, Tiwari and Lata (2018) stated that plants resort the mercury toxicity by induction of oxidative stress

enzymes such as SOD, APX, catalase, glyoxalase and GR. They also trigger the stress-responsive proteins and hormones. Various signaling cascades are stimulated by encountering heavy metal ions, namely calcium-dependent signaling and mitogen-activated protein kinase (MAPK) signaling. Chen *et al.* (2014), observed that mercury toxicity activates the biosynthesis of aromatic amino acids (tryptophan and phenylalanine), calcium accumulation and stimulates MAPK in rice. Cargnelutti *et al.* (2006), Marrugo-Negrete *et al.* (2016), Teixeira *et al.* (2018) and increased lipid peroxidation Cho and Park (2000). A high Hg content in plants affects the activity of most enzymes. The total activity of stress indicators such as superoxide dismutase (SOD), peroxidase (POD) and ascorbate peroxides (APX) increased after Hg treatment, but the vast majority of enzymes were inhibited at higher concentrations Manikandan et al. (2015) Mahbub *et al.* (2017); Zhou *et al.* (2007).

7. Mercury and their effects on plants physiology

Harmful effects of mercury lead to the inhibition of the growth and changes in biochemical constituents of food crops. Several biochemical reactions happen due to the metallic accumulation such as lipid peroxidation, enzyme activation, chromosomal aberrations, and untimely cell death. Mercury causes a decrease in photosynthetic rate that turns the colours of the plants to pale yellow. Chlorophyll synthesis in the leaves was suppressed by mercury toxicity and increases the rate of oxidizing enzymes. Mitotic behavior as well as leakage of metabolites was adversely affected due to mercury toxicity. Review intends to understand the toxic effects occurring due to mercury accumulation and morphological, physiological, and biochemical changes occurring in different food crops.

7.1. Mercury and their effects on seedling germination and growth.

Seedling growth inhibition has been observed in many plants on treatment with mercuric chloride ($HgCl_2$). The concentration of $HgCl_2$ played an important factor in the inhibition rate of germination. The concentration of $HgCl_2$ is directly proportional to the inhibition of seedling growth. Root elongation is a crucial growth affected by mercury treatment, explaining the inhibition rate observed in *Vigna radiata* under mercurial treatment that will help to understand the inhibition caused by germination rates of plants. The seed germination rate, as well as the growth rate, comparing with different concentrations of $HgCl_2$ compared with the distilled water control. Mercury treatments were done in a dilute form of mercuric chloride with different concentrations and were observed that with a lesser concentration of $HgCl_2$, there was less or no significant inhibition but as the concentration of $HgCl_2$ increased, there was a reduction in root length. Therefore, a conclusion was drawn that an increase in the concentration of mercury treatment caused significant reductions in the seedling length of mung bean seeds as compared to the control. A piece of evidence was if on the treatment of $HgCl_2$ with a high percentage there was a decrease in seed germination that lead to inhibitory responses in plant growth and development.

Mei *et al.* (2021) reported that cotton is a potential and excellent candidate to balance both agricultural production and remediation of mercury-contained soil, as its main production fiber hardly involves into food chains. However, in cotton, there is known rarely about the tolerance and response to mercury (Hg) environments. In this study, the biochemical and physiological damages, in response to Hg concentrations (0, 1, 10, 50 and 100 μM), were investigated in upland cotton seedlings. The results on germination of cotton seeds indicated the germination rates were suppressed by high Hg levels, as the decrease of percentage was more than 10% at 1000 μM Hg. They also reported that shoots and roots' growth were significantly inhibited over 10 μM Hg. The inhibitor rates (IR) in fresh weight were close in values between shoots and roots, whereas those in dry weight the root growth were more obviously influenced by Hg Fig. (25), they also stated that effects of Hg on cotton growth treated plants were inhibited under Hg stress, which may indicate the decline on assimilations regarding photosynthesis. The phenotypes on leaf surface, as well as pigments and gas exchange involved in photosynthesis, were studied. Comparing, much severe sick phenotypes appeared on leaves under higher Hg concentration. At 10 μM Hg, small white zone emerged on the leaf upper surface, whereas obvious necrosis and shrinking happened at 50 and 100 μM Hg. Obviously, the extent of leaf health inversely synchronized to the IR depending on Hg levels Fig. (26).

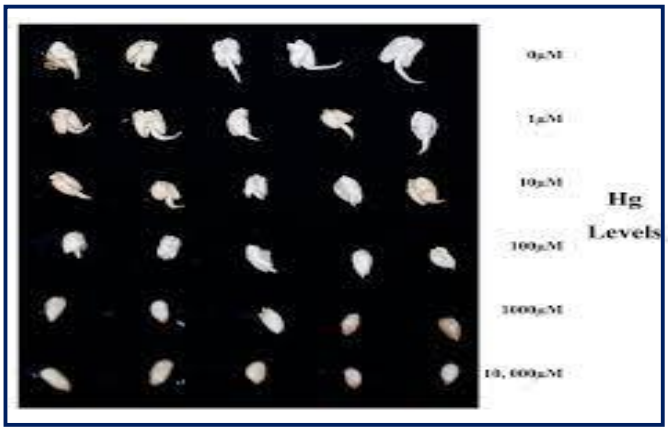

Fig. 25: Morphology on germination of decoated seeds TM-1 under Hg treatments. Decoated seeds exposed to Hg^{2+} solution with gradient 0, 1, 10, 100, 1000 and 10,000 µM, which were presented from upper to lower rows respectively. After: Mei *et al.* (2021)

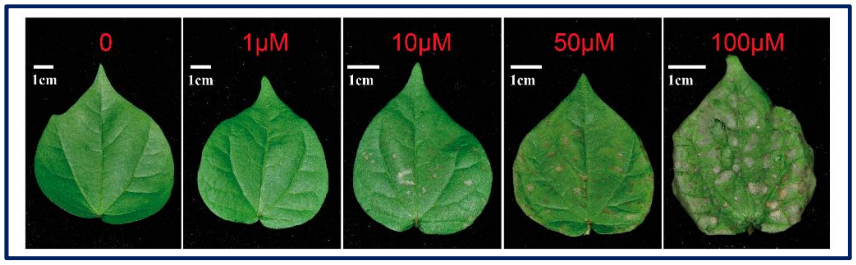

Fig. 26: Illustrates the morphological leaves responding to Hg levels at 0, 1, 10, 50 and 100 µM. After: Mei *et al.* (2021)

Comparison of organs, the growth inhibition ranked as root > leaf > stem. The declining of translocation factor (TF) opposed the Hg level as even low to 0.05 at 50 µM Hg. The assimilation in terms of photosynthesis, of cotton plants, was affected negatively by Hg, as evidenced from the performances on pigments (chlorophyll a and b) and gas exchange (Intercellular CO_2 concentration (Ci), CO_2 assimilation rate (Pn) and stomatal conductance (Gs)). Sick phenotypes on leaf surface included small white zone, shrinking and necrosis. Membrane lipid peroxidation and leakage were Hg dose-dependent as indicated by malondialdehyde (MDA) content and relative conductivity (RC) values in leaves and roots. More than 10 µM Hg damaged antioxidant enzyme system in both leaves and roots ($p < 0.05$). Concluding, 10 µM Hg post negative consequences to upland cotton plants in growth, physiology and biochemistry, whereas, high phytotoxicity and damage appeared at more than 50 µM Hg concentration.

7.2. Impact of mercury on chlorophyll and photosynthesis

Heavy metals have always dominated the biota since they are always present in elevated amounts. Heavy metals cannot be decomposed in nature and it can only be translocated into plants and transferred further into the human food chain Patra and Sharma (2000). The processes by which heavy metals are transferred to plants are (**a**) phytoextraction (phytoremediation sub process in which plants remove dangerous components from contaminated soil), (**b**) Phyto stabilization (immobilization and reduction of the mobility of heavy metals in soil), and (**c**) rhizofiltration (a form of phytoremediation to use plant roots to absorb the toxic substances). Through transference in the food chain, these metals harm plants and extend to harming human health Cho-Ruk *et al.* (2006). Leaves play an important role in capturing light and making their own food via photosynthesis. Photosynthesis is a hypersensitive process that is interfered with either by heavy metal invasion that leads to the inhibition of enzymatic steps directly or by inducing the deficiency of an important nutrient Sloan *et al.* (2001). It has been observed that Hg

affects the level of phosphorus and manganese contents in plants that in turn reduces the chlorophyll content and increases the malondialdehyde (MDA) and thiol levels Van Assche and Clijsters (1990). A report on the chlorophyll contents of wheat upon treatment with Hg showed that in the initial days of treatment, there was an increase in the content of chlorophyll a, chlorophyll b, and total chlorophyll with the increasing concentration of Hg but later on the content of chlorophyll a, chlorophyll b, and total chlorophyll have decreased significantly with the increasing rate of Hg which states that both low and high concentration of Hg will stimulate or inhibit the chlorophyll synthesis level at early stages of the wheat growth while on the later stages of the wheat growth not only less but also a high concentration of Hg will lead to inhibition of chlorophyll synthesis. In the cells of Chlorella, pyrenoidosa that the color of the leaves turned pale–yellow on treatment with Hg and a significant fall in photosynthetic rate noticed Moreno-Jiménez *et al.* (2009). Yadav *et al.* (2016) stated that toxicity of heavy metals in plants and role of mineral nutrients in its alleviation. Heavy metal contamination in our environment has become a huge problem for all living things. Heavy metals comprise of an imprecise group of elements, such as lead (Pb), chromium (Cr), arsenic (As), zinc (Zn), cadmium (Cd), copper (Cu), mercury (Hg) and nickel (Ni). These contaminants occur due to the hastened rate of industrialization and enormous usage of pesticides in agriculture. Mining, gasoline, paints, sewage, sludges; coal combustion rock weathering are some of the other sources through which these contaminants get entry into the ecosystem Khan *et al.* (2008), Zhang *et al.* (2010). Heavy metals are also deemed trace elements because of their minimal, but indispensable requirement in plant growth and development Kabata-Pendias (2010). These HMs have immense roles in biochemical and physiological functions and are important constituents of various key enzymes and redox reactions when present in limited concentrations Tchounwou *et al.* (2012).

Mao *et al.* (2021) reported that this is a novel study about responses of leaf photosynthetic traits and plant mercury (Hg) accumulation of rice grown in Hg polluted soils to elevated CO_2 (ECO_2). The aim of this study was to provide basic information on the acclimation capacity of photosynthesis and Hg accumulation in rice grown in Hg polluted soil under ECO_2 at day, night, and full day. For this purpose, we analyzed leaf photosynthetic traits of rice at flowering and grain filling. In addition, chlorophyll content, soluble sugar and malondialdehyde (MDA) of rice leaves were measured at flowering.

Seed yield, ear number, grain number per ear, 1000-grain weight, total mercury (THg) and methylmercury (MeHg) contents were determined after harvest. The results showed that Hg polluted soil and ECO_2 had no significant effect on leaf chlorophyll content and leaf mass per area (LMA) in rice. The contents of soluble sugar and MDA in leaves increased significantly under ECO_2. Mercury polluted soil treatment significantly reduced the light saturated CO_2 assimilation rate (Asat) of rice leaves only at flowering, but not at grain filling. Night ECO_2 greatly improved rice leaf water use efficiency (WUE). ECO_2 greatly increased seed yield and ear number. In addition, ECO_2 did not affect THg accumulation in rice organs, but ECO_2 and Hg treatment had a significant interaction on MeHg in seeds, husks and roots. They also reported that attention should be payed to crop MeHg contents since ECO_2 could increase MeHg in Hg polluted regions. This will increase rice consumers' Hg exposure risk. According to this study, rice yield may be underestimated at elevated CO2 ECO_2, because elevated CO2 ECO_2 increased rice yield at daytime, full day even nighttime. In addition, rice growth with Hg under elevated CO2 ECO_2 at daytime and nighttime increased the seed yield of rice plants. Elevated CO2 ECO2 did not enhance the accumulation of THg, but the MeHg content in seeds was increased. Thus, elevated CO2 ECO_2 may change the Hg accumulation form in rice plants. Rice without Hg exposure had a higher assimilation rate (Asat) at flowering and a lower assimilation rate (Asat) at grain filling, but exposure to Hg reduced assimilation rate Asat as a consequence of Hg accumulation.

Since the industrial revolution, with large-scale use and emission of mercury (Hg), the Hg pollution has obtained much attention due to its harmful effects on the ecological environment and human health Benoit *et al.*, (1998), Ma *et al.*, (2019b), 2019a, (2016). Mercury is persistent of migration, with high toxicity and bioaccumulation characteristics Li *et al.*, (2019); Ma *et al.*, (2019b); Wu *et al.*, (2018b); Zhao *et al.*, (2019). Though Hg is a stubborn pollutant, studies tried to moderate the activity of mercury by using nanoparticles, biochar, sulfur or selenium to de-contamination the water and soil pollution Karimi-Maleh *et al.*, (2020c), Li *et al.*, (2019); Xing *et al.*, (2019). The Hg is a worldwide toxic pollutant, especially the exposure to humans to methylmercury (MeHg) Abeysinghe *et al.*, (2017); Ma *et al.*, (2019b), Tang *et al.*, (2020). Recently, it has been reported that the source of human Hg exposure is not only intake of fish resources, but also of rice in Hg contaminated areas Ma *et al.*, (2019b);

Rothenberg *et al.*, (2014); Tang *et al.*, (2018); Wu *et al.*, 2018a, (2018b). Rice is an important food crop, and about half of the world's population supply with food fully depends on rice products. In Asia, the rice cultivation area is very large and rice constitutes the main food Abeysinghe *et al.*, (2017); Zhao *et al.*, (2019). The rice planting area in East Asia accounts for the largest area in the world and also is the most essential rice eating area Rothenberg *et al.*, (2014); Xing *et al.*, (2019) Xu *et al.*, (2017). Planting rice in Hg polluted land will lead to the enrichment of a large amount of Hg in rice, which is harmful to its consumers Wu *et al.*, (2018b; Zhao *et al.*, 2016a, (2016b). Cui *et al.* (2022) reported that rice grain consumption is a primary pathway of human mercury exposure, in China to trace the source of mercury in rice grain; we developed a rice paddy mercury transport and transformation model with a grid resolution of 1 km × 1 km by using the unit cell mass conservation method. Fig. (27). The total mercury (THg) and methylmercury (MeHg) concentrations in Chinese rice grain ranged from 0.08 to 243.6 and 0.03 to 238.6 µg/ kg, respectively, in 2017. Approximately, 81.3% of the national average rice grain THg concentration was due to atmospheric mercury deposition. However, soil heterogeneity, especially, the variation in soil mercury, led to the wide rice grain THg distribution across grids. Approximately, 64.8% of the national average rice grain MeHg concentration was due to soil mercury. In situ methylation was the main pathway via which the rice grain MeHg concentration was increased.

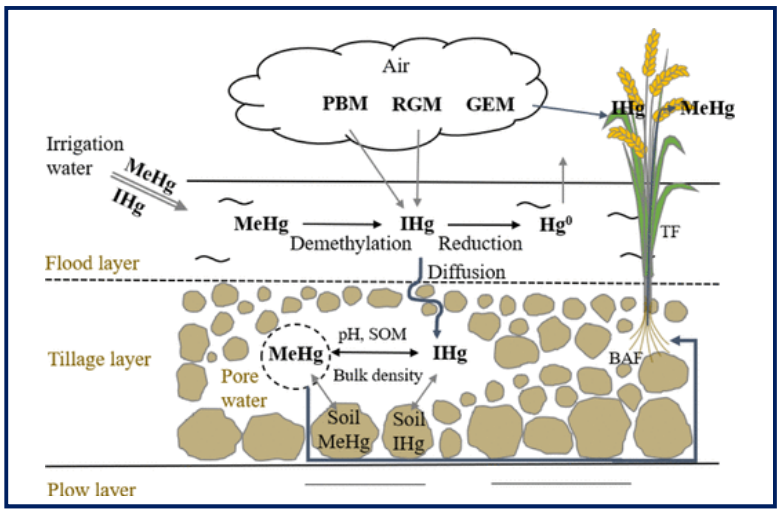

Fig. 27: Illustrates mercury transport and transformation in rice paddies. [(1) Mercury input: PBM and RGM deposition into the floodwater; GEM deposition into rice plants; and irrigation water input and soil mercury desorption. (2) Transport and transformation in rice paddies: demethylation and reduction in the floodwater and diffusion, adsorption, methylation, and demethylation in the tillage layer. (3) Accumulation in rice grain: MeHg absorbed by roots and transported to rice grain and IHg absorbed from air. PBM: particle-bound mercury; RGM: reactive gaseous mercury; GEM: gaseous elemental mercury; MeHg: methylmercury; IHg: inorganic mercury; SOM: soil organic matter; BAF: bioaccumulation factor of roots; TF: transport factor; and LAI: leaf area index].After: Cui *et al.* (2022)

The coupled impact of high mercury input and methylation potential led to extremely high rice grain MeHg in partial grids among Guizhou province and junctions with surrounding provinces. The spatial variation in soil organic matter significantly affected the methylation potential among grids, especially, in Northeast China. Based on the high-resolution rice grain THg concentration, we identified 0.72% of grids as heavily polluted THg grids (rice grain THg > 20 µg/kg). These grids mainly corresponded to areas in which the human activities of nonferrous metal smelting, cement clinker production, and mercury and other metal mining were conducted. Thus, we recommended measures that are targeted at the control of heavy pollution of rice grain by THg according to the pollution sources.

On the other hand, atmospheric CO_2 has increased dramatically in the past few centuries IPCC *et al.* (2013). This increasing trend is projected to continue throughout this century. Former studies showed that elevated CO_2 concentration (ECO_2) can greatly increase leaf photosynthetic rates and seed yield (Ainsworth *et al.* (2008a), (2002); Ellsworth *et al.* (2004); Kitaoka *et al.* (2016), Watanabe *et al.*

(2016). In most of these studies, plants were exposed to ECO_2 either at daytime or for the full day (Bunce (2003); Ellsworth *et al.* (2017), (2012); Hoshika *et al.* (2012); Kazemi *et al.* (2018). Therefore, physiology responses to night ECO_2 are largely unknown Bunce (2017), (2002) and (2005). It is important to elucidate such responses, since leaf respiration during the night counteracts carbon accumulation by photosynthesis at daytime. Fossil fuel combustion would release both CO_2 and Hg to the atmosphere, with the consequence of enhanced soil Hg under ECO_2 Bunce (2017). Former in-situ studies reported that soil Hg accumulations were almost 30% greater under ECO_2 in temperate forests ecosystems, but similar information on herbaceous crop plants is lacking (Bunce (2017). Numerous studies have focused on the independent effects of ECO_2 and Hg on plant physiology Ainsworth (2016); Ainsworth *et al.* (2008b); Frossard *et al.* (2017); Kazemi *et al.* (2018); Lv *et al.* (2020); Xiong *et al.*, (2019). However, there is much less information on the effect of ECO_2 levels combined with Hg pollution on leaf photosynthesis and grain yield, particularly for effects at night Bunce (2005); Xiong *et al.* (2019). Here, we tested whether ECO_2 released at daytime, during the nighttime, or during the full day induces differences in grain yield and leaf photosynthetic traits of rice. Since there is no information about the responses of herbaceous plants to Hg contamination under ECO_2, this study aims to fill the knowledge gap of Hg absorption by rice under ECO_2 and its physiological responses to this treatment. Therefore, the specific objectives of this study were to elucidate under ECO_2 at day, night or full day, whether rice (1) has higher leaf net photosynthesis (Asat), stomatal conductance (gs), transpiration (E), water use efficiency (WUE) and seed yield, and (2) accumulates more Hg from contaminated soils.

8. Biochemical toxicity of mercury in medicinal plants

Plants are the storehouse of natural biochemical. To produce the necessary biochemical, plants rely on the most sophisticated metabolism for the regulation of their growth, development, and all those environmental interactions happening around which produces plant hormones, vitamins, and distinct phytochemicals via its primary and secondary metabolic processes. The production of essential phytochemicals has mediated by medicinal plants. Therefore, the proper regulation of the plant biochemical is very necessary but the exposure of plants to heavy metals such as mercury that is considered the most persistent toxic metal causing alteration in the regulatory metabolism happening in the medicinal plants.

Mercury present in the medicinal plant stimulates the production of bioactive compounds that interrupt the regulation of the phytochemicals. The oxidative stress induced due to mercury accumulation triggers signaling pathways that eventually affects the production of specific plant metabolites. To be specific reactive oxygen species (ROS), initiated during mercurial stress causes lipid peroxidation that stimulates the configuration of highly active signaling compounds that are capable of triggering the production of bioactive compounds Kamp-Nielsen (1971). Lian-Jiu *et al.* (2019) reported that reactive oxygen species (ROS) induced lipid peroxidation plays a critical role in cell death including apoptosis, autophagy, and ferroptosis. This fundamental and conserved mechanism is based on an excess of ROS that attacks bio membranes, propagates lipid peroxidation chain reactions, and subsequently induces different types of cell death. A highly evolved sophisticated antioxidant system exists that acts to protect the cells from oxidative damage. In this review, we discussed how ROS propagate lipid peroxidation chain reactions and how the products of lipid peroxidation initiate apoptosis and autophagy in current models. We also discussed the mechanism of lipid peroxidation during ferroptosis, and we summarized lipid peroxidation in pathological conditions of critical illness. We aim to bring a more global and integrative sight to know how different ROS-induced lipid peroxidation occurs among apoptosis, autophagy, and ferroptosis. They also stated that ROS are partially, reduced oxygen containing molecules, which are free radicals and/or oxygen derivatives, including superoxide anion, hydrogen peroxide, hydroxyl radical, lipid hydro peroxides, and peroxyl radicals. Most intracellular ROS are derived from superoxide radical, whose formation is mainly through NADPH oxidases (NOXs), xanthine oxidase (XO), and the mitochondrial electron transport chain (mETC) in endogenous biologic systems Sakellariou *et al.* (2014), Guerriero *et al.* (2014). Reactive oxygen species are converted to hydrogen peroxide by the superoxide dismutase (SOD) and yield the highly toxic hydroxyl radical in the presence of reduced iron (Fe^{2+}) through the Fenton reaction which have different peroxide species to generate hydroxyl (· OH) or alkoxyl (RO·) radicals Wen *et al.* (2013) . Ferric iron (Fe^{3+}) can be recycled to Fe^{2+} via the Haber-Weiss reaction by oxidation with a peroxyl radical to oxygen Doll and Conrad (2017), Kruszewski (2003) Fig. (28). Imbalance in the

rate of ROS generation leads to oxidative stress and consequent production of free radicals that can damage DNA, proteins, and lipids Latunde-Dada (2017).

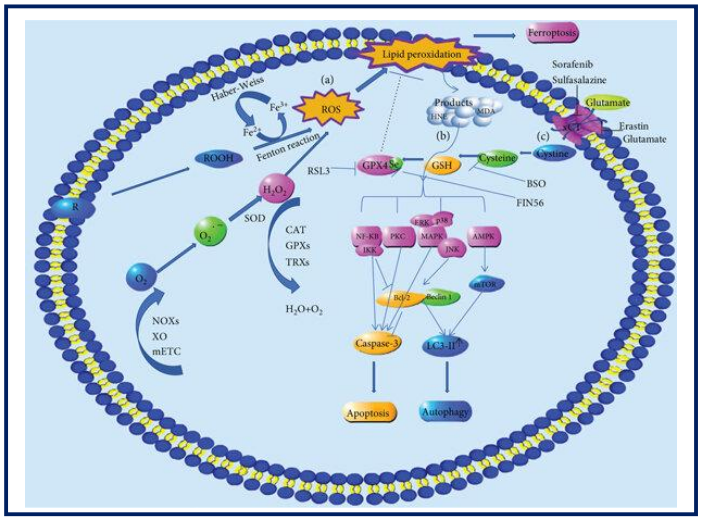

Fig. 28: Illustrates generation of ROS and lipid peroxidation in cell death. (a) Generation of ROS; ROS are derived from superoxide radical, whose formation is mainly through NADPH oxidases, xanthine oxidase, and the mitochondrial electron-transport chain. Polyunsaturated fatty acids containing phospholipids can generate alkoxyl (RO·) radicals by Fenton chemistry reaction. (b) The products of lipid peroxidation induce apoptosis and autophagy via different pathways. (c) GPX4 activity decreases and a depletion of GSH causes lipid peroxidation and consequently to ferroptosis. After: Lian-Jiu *et al.* (2019)

Hélio *et al.* (2013) reported that UV radiation is divided into three classes: UV-C, UV-B, and UV-A. Although the highly energetic UV-C (200–280 nm) is completely absorbed by atmospheric gases and UV-A (315–400 nm) is hardly absorbed by ozone, the potentially harmful UV-B (280–320 nm) is only partially absorbed by atmospheric ozone, comprising approximately 4% of terrestrial radiation. In the last 20 years, the depletion of the stratospheric ozone layer, catalyzed by chlorofluorocarbons and other pollutants, resulted in rising levels of the sun's UV-B radiation reaching the Earth's surface. Due to the high energy of UV-B radiation, even modest increases could lead to significant biological damage Jansen *et al.* (1998); Frohnmeyer and Staiger (2003). Elevations of UV-B radiation levels have effects on plant development, morphology, and physiology. Such responses include inhibition of plant growth rates, biomass reduction, increased accumulation of UV absorbing secondary metabolites, and influence on numerous ecological processes. In addition to indirect changes, caused by affecting host plant quality, predators, and pathogens, UV-B radiation may directly cause modifications in herbivore behavior and physiological processes Julkunen-Tiitto *et al.* (2005); Tuteja *et al.* (2009). As sessile organisms, plants are exposed to various environmental factors that lead to changes in physiology and morphology. One of the most relevant of these factors is ultraviolet radiation, on which significant advances have been achieved, in both understanding effects on plants and describing response mechanisms. UV-B radiation can inhibit growth and decrease leaf area, but also increase parameters such as leaf number, secondary branch number, and leaf weight per plant. Other aspects of leaf morphology can also change upon UV-B exposure, including presence of particulate matter in substomatic chambers Zu *et al.* (2010), and accumulation of epicuticular wax crystalloids on the leaf surface, reflecting solar radiation Barnes *et al.* (1996). UV-A and UV-C radiation affected the structure and ultrastructure of *Capsicum longum*, leading to a decrease in shoot growth and leaf area, whereas, stem and leaf thickness, as well as stomata number and size significantly increased. UV treatment also caused thylakoid expansion, starch reduction, and formation of crystals in peroxisomes of mesophyll cells Sarghein *et al.* (2011). Plants have protective mechanisms, both constitutive and induced, or can

activate repair responses to cope with UV-B stress. One of the most common protective responses is the accumulation of secondary metabolites capable of absorbing radiation in the ultraviolet wavelength range, such as anthocyanins, flavonols, and flavones, which can scavenge free radicals, mainly ROS Hahlbrock and Scheel (1989). Plants can also produce antioxidant enzymes, such as catalases, peroxidases, and superoxide dismutases, to scavenge these free radicals and protect cellular integrity Heinonen *et al.* (1998). Differences in defense responses, as well as in their kinetics and intensity, can be the reason for some plants being highly resistant to UV radiation compared to others Fig. (29). Pandey *et al.* (2023) stated that UV-B and heavy metals cause alterations in the secondary metabolites of medicinal plants, they found that UV-B and heavy metal stress activate a signal transduction pathway that consequently, leads to alterations in the expression of various genes of the enzymes taking part in the biosynthesis of secondary metabolites in medicinal plants.

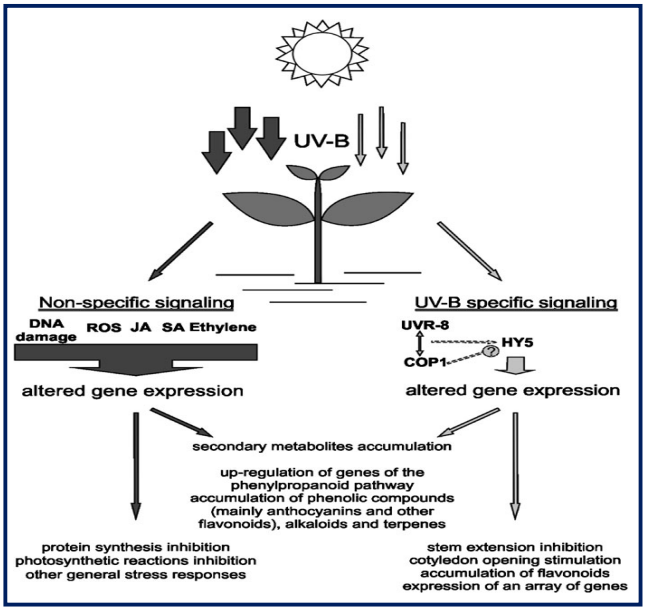

Fig. 29: Illustrates a schematic representation of main UV-B signal transduction pathways in plants. Low levels of UV-B (light-colored arrows) may mediate UV-B specific pathways, differently from general stress responses, generated under high levels of radiation (dark arrows). These pathways change the expression of an array of genes, with both specific and/or overlapping responses. Dashed lines indicate incompletely understood correlations. Data to date indicates that UVR8 monomerization and UVR8- COP1 interaction are UV-B dependent processes that lead to HY5 gene transcription. HY5 protein then regulates downstream target genes involved in UV photomorphogenic responses, including UV protection genes, such as those encoding enzymes of the flavonoid pathway. ROS: reactive oxygen species; JA: jasmonic acid; SA: salicylic acid; UVR8: UV RESISTANCE LOCUS8; COP1: CONSTITUTIVELY PHOTOMORPHOGENIC1; HY5: ELONGATED HYPOCOTYL5. After: Hélio *et al.* (2013)

However, these alterations in biosynthesis and accumulation of secondary metabolites range from having positive to negative to no effects, depending on various other factors. Including species, cultivars, dose and duration, developmental stages, experimental conditions and various environmental variables. In addition, as there are not many data available regarding the interactive effect of heavy metals and UV-B on medicinal plants, it is not completely clear whether the two stresses (UV-B and heavy metals) act synergistically or antagonistically. However, the interactive effect mostly showed a synergistic effect on the formation of secondary metabolites in medicinal plants. Furthermore, there is a need to explore interactive studies involving different doses of heavy metals and UV-B radiation on various medicinal plants under varied environments to unravel the precise mechanism behind this stimulation. Moreover, understanding how UV-B and heavy metals both individually and in combination influence the accumulation of secondary metabolites in medicinal plants can help us to

assess these metabolites' biological functions, and can offer standards for specifying the ideal quality and yields of medicinally important compounds. They also reported that various secondary metabolites are present in plants, and consumers are becoming more interested in them because of the extensive usage of plants in the pharmaceutical industry. These secondary metabolites possess various pharmaceutical activities; due to this, they are widely used in the treatment of various disorders of human beings. The WHO estimates that 60% of people worldwide and 80% of human beings in developing countries still rely on herbal remedies. Due to their minimal side effects, the demand for medicinal plants has dramatically increased in recent years, and interest in their use has increased locally, nationally and globally Mahajan *et al.* (2020). These secondary metabolites frequently exhibit multiple functionalities and typically contain more than one functional group. Even though secondary metabolites are structurally diverse compounds, they are derived from limited products of primary metabolism Ncube *et al.* (2012). Broadly, secondary metabolites are classified into three groups, phenolics, terpenoids and nitrogen-containing compounds Fig. (30).

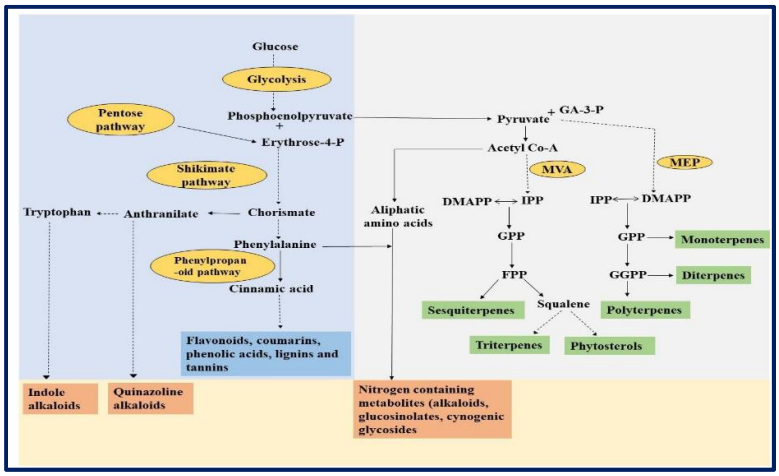

Fig. 30: Schematic overview of biosynthesis of different groups of secondary metabolites and their interrelationship with primary metabolism, modified from Mahajan *et al.* (2020) Jan *et al.* (2021). Abbreviations: MVA- Mevalonic acid pathway; MEP-Methylerythritol phosphate pathway; IPP-Isopentenyl pyrophosphate; DMAPP-Dimethylallyl pyrophosphate; GPP-Geranyl pyrophosphate; FPP-Farnesyl pyrophosphate; GGPP-Geranylgeranyl pyrophosphate. After: Pandey *et al.* (2023)

Terpenoids are synthesized by the plastidic MEP (Methylerythritol phosphate) and cytosolic MVA (Mevalonic acid) pathway, which utilizes Dimethylallyl pyrophosphate (DMAPP) and Isopentenyl pyrophosphate (IPP) moieties, respectively, which serve as fundamental building blocks of all isoprenoid. The MEP pathway leads to the generation of mono, di, tetra and polyterpenes, while the MVA pathway results in the synthesis of sesquiterpenes, diterpenes and phytosterols Pandey *et al.* (2021), Mahajan *et al.* (2020). Another important group of secondary metabolites is phenolics that are generally divided into five subgroups, flavonoids, phenolic acid, lignin, coumarins and tannins. Phenolics are synthesized through the phenylpropanoid pathway by utilizing phenylalanine as a key precursor molecule, which in turn is synthesized via the shikimic acid pathway by the reaction of erythrose-4-phosphate and phosphoenolpyruvate. Nitrogen-containing metabolites are also one of the potential groups of secondary metabolites including alkaloids, cyanogenic glycoside. In general, the various essential roles that secondary metabolites play in plant-environment interaction are associated with their occurrence in a variety of cellular and subcellular compartments. Agati *et al.* (2012) revealed that dihydroxy B-ring-substituted flavonoids localized to the chloroplasts, vacuoles and the nucleus, and may effectively scavenge ROS from these sites. In addition, Facchini (2001) reported that several enzymes that are involved in the biosynthesis pathway of different alkaloids localized in various subcellular compartments, such as enzymes of vindoline (a terpenoids indole alkaloid) biosynthesis in *Catharanthus roseus*, are localized to not less than five subcellular compartments. Similarly, the biosynthesis of quinolizidine alkaloids in a legume, namely lupin, occurs in the chloroplast of mesophyll

cells Facchini (2001). Much less numerous are the studies related to localization of secondary metabolites in subcellular compartments concerning the effects of abiotic stresses, particularly, UV-B and heavy metals. Zagoskina *et al.* (2003) observed that, exposure of the callus culture of *Camellia sinensis* to UV-B cause's enhanced accumulation of phenolic acids in intercellular spaces and cell walls, and accumulation of lignin on the surface of the callus culture Zagoskina *et al.* (2003). Inhibition of photophosphorylation involved with noncyclic electron transport was observed in spinach plants due to mercury addition that also marked the interruption of the photophosphorylation rate by mercury.

9. Impacts of mercury on enzymes.

The enzymes glutamine synthetase (GS), glutamate synthase (GOGAT), glutamate dehydrogenase (GDH), and nitrate reductase (NR) are responsible for the biosynthesis of nitrogen-carrying amino acids Lam (1996). Nitrate reductase (NR, EC 1.6.6.1) is a complex enzyme characterized as a SH containing molybdoflavohemoprotein Hewitt and Nottan (1979). Nitrate is currently one of the most hazardous pollutants Awasthi and Rai (2005). Nitrate reductase is substrate inducible and involves de novo synthesis of the enzyme in response to nitrate Zielke and Filner (1971), Somers *et al.* (1983). Nitrate reduction catalyzed by this enzyme is considered as the rate-limiting step in the overall process of nitrate assimilation pathway Srivastava (1980), Lin *et al.* (2020) it is important to understand the biochemical mechanism for nitrate uptake and assimilation including different pathway regulations in these plants. Nitrate uptake in plants is a protein-mediated process and assimilation of nitrate requires three enzyme-dependent conversions. The process was shown in Fig. (31).

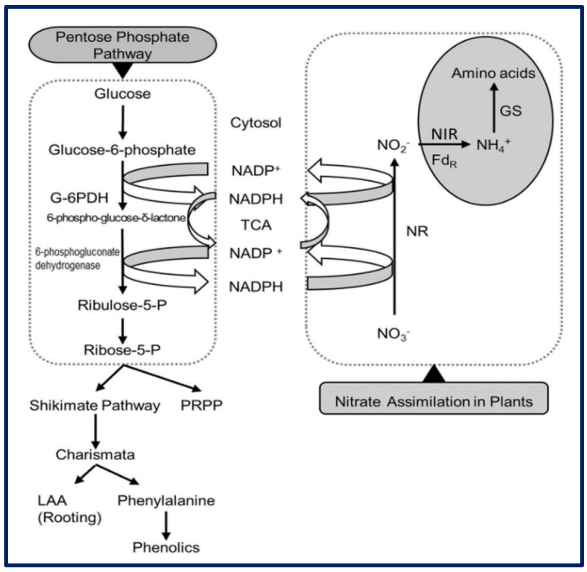

Fig. 31: Illustrates the relation of the enzymes with nitrogen assimilation and pentose phosphate pathway. After: Lin *et al.* (2020).

Driving pentose phosphate pathway can provide energy (NADPH) for nitrate assimilation and provide growth regulators and phenols needed by plants. Enzymes are essential catalysts for these processes, such as SDH that promotes the production of NADPH in the TCA process. Firstly nitrate (NO^-_3) is reduced to nitrite (NO^-_2) by the nitrate reductase (NR), next, the nitrite (NO^-_2) is converted to ammonium (NH^+_4) by nitrite reductase (NIR), and lastly, ammonium is reduced into amino acids with glutamine synthetase/glutamate synthase Farr *et al.* (1994) .The efficient utilization of absorbed nitrate in plants largely relies on the efficiency of reducing nitrate to ammonium and ammonium into amino acids Jiang *et al.* (2002). In the synthesis of nitrate reductase, light is the most important factor in regulating the supply of reductant in this process. Many studies reported that NADPH produced by the oxidative pentose phosphate pathway could act as an alternative to reducing equivalent for nitrate reduction in dark Huppe *et al.* (1994), Pattanayak and Chatterjee (1998). Electrons from NADPH must

be found to reduce Fd, which act as electron donor to nitrate reductase. Onset of nitrate (NO_3^-) assimilation is in accordance with the Fd thioredoxin-dependent activation of glucose-6-phosphate dehydrogenase (G6PDH), the regulatory enzyme of the oxidative pentose phosphate pathway Huppe *et al.* (1994), Farr *et al.* (1994). Oxidation of carbohydrate through the oxidative pentose phosphate pathway also gives reducing power for nitrite (NO_2^-) reduction Bowsher *et al.* (1989), Bradford (1976). Pentose phosphate pathway can generate NADPH, which can be utilized for nitrate reduction in the cytosol. The conversion to ribulose - 5 - phosphate along with generation of NADPH by G6PDH is the first committed step of pentose phosphate pathway Sarkar and Shetty (2011). Pentose phosphate pathway acted on the shikimate and phenylpropanoid pathways, accumulated phenolic phytochemicals in plants by direct generation or regulatory of the pathway Sarkar and Shetty (2011). Lin *et al.* (2010). Proline synthesis during microbial interaction and proline analogue treatment drives the utilization for NADPH and provide NADP+, which is cofactor for G6PDH Sarkar and Shetty (2011 Sarkar *et al.* (2009) . Therefore, it may improve cellular NADP+ / NADPH ratio, which could stimulate G6PDH.

As a result, deregulation of the pentose phosphate pathway may stimulate anabolism of erythrose-4-phosphate for biosynthesis of shikimate and phenylpropanoid metabolites Sarkar and Shetty (2011), Jiang and Zhang (2016) Meanwhile, proline acts as a reducing equivalent, in place of NADH to synthesize ATP through oxidation phosphorylation in the mitochondria Sarkar and Shetty (2011)., Rayapati and Stewart (1991). The relation of the enzymes with nitrogen assimilation and the pentose phosphate pathway was shown in Fig. (32). According to the correlation between the biosynthesis of exogenous lypsy phenolic. Substances and the reaction of plant antioxidant enzymes, a model of action of phytophenolmetabolites is proposed Sarkar and Shetty (2011), Lin *et al.* (2010). Sarkar *et al.* (2012). Through adopting more effective strategies, high nitrate concentration in water and soil also could produce similar reaction in plants and plants could tolerate stress. The early growth period is vital for any plant under nitrate stress, especially, from germination to development of first two leaves. During early growth stages, nitrate assimilation of plants combined with proline-associated pentose phosphate pathway could provide a better defensive strategy against high nitrate concentrations. We predicted that the research on three feed-plant species including alfalfa (*Medicago sativa* L.), tall fescue (*Festuca arundinacea* L.) and perennial ryegrass (*Lolium perenne* L.) could clarify the relation of nitrate assimilation and proline-associated pentose phosphate pathway and mechanism of these feed-plant species to defend high nitrate concentrations. The efficient utilization of absorbed nitrate in plants largely relies on the efficiency of nitrate reduction to ammonium and ammonium assimilation into amino acids, which are largely relevant to nitrate reductase activity. Photochemical efficiency has been chosen as light is important in the synthesis of nitrate reductase. Oxidation of carbohydrate through the oxidative pentose phosphate pathway gives reducing power and G6DPH is the regulatory enzyme in this procedure, so the G6DPH is a key factor in nitrite (NO_2^-) reduction. In view, that proline can scavenge reactive oxygen species as a reductant, proline-linked pentose phosphate pathway stimulates the generation of total soluble phenolics that plays an important role in countering oxidative stress, the proline content, and total soluble phenolics content was measured in the study. SDH relate to TCA cycle that can produce NADH as reductant. The activity of key antioxidant enzymes such as SOD, CAT, GPX, can be stimulated by the proline under nitrate treatments.

In the overall strategy for checking the efficiency that plants removing the nitrate in soil and ground water nitrate removal, we have measured total soluble phenolics content, nitrate reductase activity, G6PDH, proline content, SDH, activity of critical antioxidant enzymes and photochemical efficiency, then explored the relation of nitrate assimilation and proline associated pentose phosphate pathway and mechanism of these feed-plant species defending high nitrate concentrations.

Supply of inorganic mercury inhibited substantially in vivo as well as in vitro NR activity and endogenous nitrate pool in excised bean leaf segments. Though in vitro specific activity of the enzyme remains unchanged, it has been suggested that mercury has an inhibitory role on NR activity in bean leaf segments Vyas and Puranik, (1993). Application of mercury to excised bean leaf segments increased glutamate dehydrogenase (NADH-GDH, EC 1.4.1.3) activity substantially. However, specific activity of the enzyme decreased at lower concentration of mercury and increased to a lesser extent at higher concentration of mercury Fig. (32).

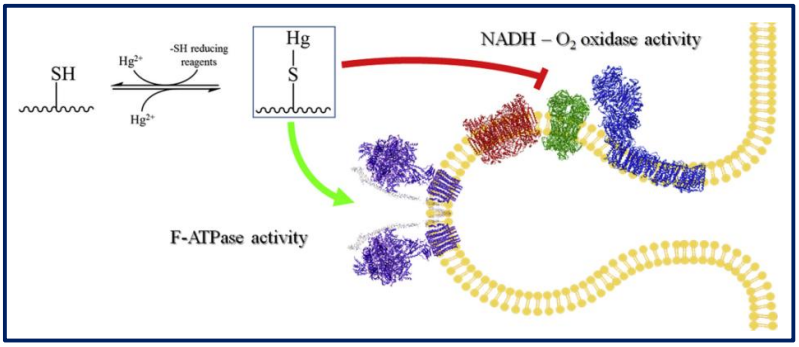

Fig. 32: Illustrates mercury and protein thiols: Stimulation of Mitochondrial lF1FO– ATPase and inhibition of respiration. After: Salvatore Nesci *et al.* (2016)

Salvatore Nesci *et al.* (2016) stated that in spite of the known widespread toxicity of mercury, its impact on mitochondrial is a still poorly explored topic. Even if many studies have dealt with of mitochondrial respiration, as far as we are aware Hg^{2+} effects on individual complexes are not so clear. In the present study, changes in swine heart mitochondrial respiration and F_1F_O-ATPase (F-ATPase) activity promoted by micromolar Hg^{2+} concentrations were investigated. Hg^{2+} was found to inhibit the respiration of NADH-energized mitochondria, whereas, it was ineffective when the substrate was. Interestingly, the same micromolar Hg^{2+} doses that inhibited the NADH–O2 activity stimulated the F-ATPase, most likely by interacting with adjacent thiol residues.

Tollefsen *et al.* (2017) reported inorganic mercury (IHg) is highly toxic to organisms including crustaceans and displays multiple toxic modes of action (MoA). The main aim of this investigation was to assess the acute and sublethal toxicity mediated by mercury chloride ($HgCl_2$) in the marine copepod *Calanus finmarchicus*. A combination of short-term static studies to determine acute toxicity and a transcriptional investigation to characterize the sublethal MoA of $HgCl_2$ were conducted with an in-house continuous culture of C. finmarchicus. Transcriptional changes were determined by a custom 6.6 k C. finmarchicus Agilent oligonucleotide microarray and quantitative RT-PCR analysis. Data demonstrate that $HgCl_2$ produced a concentration and time-dependent reduction in survival (NOEC48 h= 6.9 µg/L [Hg^{2+}] and LC50 of 279, 73, 48, and 34 µg/L [Hg^{2+}] after 24, 48, 72, and 96 h, respectively) and that exposure to sublethal concentrations of $HgCl_2$ (5 µg/L [Hg^{2+}]) induced differential expression of 98 features (probes) on the microarray. Gene ontology (GO) and toxicological pathway analyses suggested that the main MOA were **(A)** uncoupling of mitochondrial oxidative phosphorylation (OXPHOS) and ATP production, **(B)** oxidative stress and macromolecular damage, **(C)** inactivation of cellular enzymes, (**D**) induction of cellular apoptosis and auto phagocytosis, **(E)** over-excitation of glutamate receptors (neurotoxicity), **(F)** disruption of calcium homeostasis and signaling, and **(G)** modulation of nuclear receptor activity involved in vitamin D receptor signaling. Quantitative RT-PCR analysis verified that oligoarray performed reliably in terms of specificity and response, thus demonstrating that Hg^{2+} exerts multiple potential MoA in C. finmarchicus Fig. (33). Accordingly, Hg^{2+} dose-dependently decreased protein thiols and all the elicited effects on mitochondrial complexes were reversed by the thiol reducing agent. These findings clearly indicate that Hg^{2+} interacts with Cys residues of these complexes and differently modulate their functionality by modifying the redox state. The results, which cast light on some implications of metal-thiol interactions up to now not fully explored, may contribute to clarify the molecular mechanisms of mercury toxicity to mitochondria.

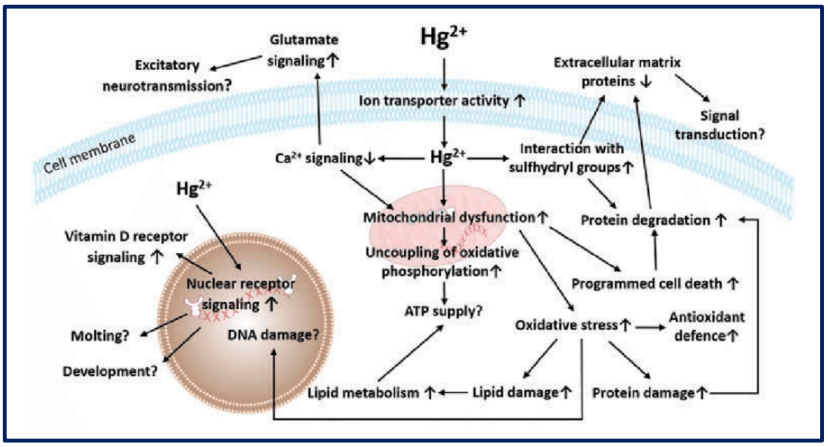

Fig. 33: Potential molecular modes of Action (MoA) of divalent mercury (Hg^{2+}) in *Calanus finmarchicus*. The results depict hypothetical MoA generated on basis of transcriptional changes observed in *Calanus finmarchicus* after 48 h exposure to 5 µg/L Hg^{2+} and review of known MoA of Hg in other eukaryotes. After: Tollefsen *et al.* (2017)

Eventually, pronounced increase in mercury activity indicated the possible role of the enzyme under mercury stress Gupta and Gadre, (2005). Mercury supply increased glutamate synthase [NAD (P) H-GOGAT, EC 1.4.1.14] Basak *et al.*, (2001) activity. It has been suggested that mercury activates the NADH-GDH enzyme by binding to thiol groups of protein. In the presence of mercury ($HgCl_2$) demonstrates Increase in NR activity by glutathione (GSH) involves its thiol groups Vyas and Puranik, (1993). GDH is found in all higher plants examined and is often present at high levels in senescing and root tissues Loyolevargas and Jiminez, (1984). One of these alternative pathways is the reaction catalyzed by the mitochondrial NAD (H)-dependent glutamic acid dehydrogenase (GDH; EC 1.4.1.2), which possesses the capacity to assimilate ammonium in vitro utilizing the organic molecule 2-oxoglutarate to synthesize glutamic acid. This observation led a number of authors to propose that GDH could operate in the direction of ammonium assimilation Yamaya and Oaks (1987); Oaks (1995); Melo-Oliveira *et al.* (1996), although all the 15N labeling experiments performed in vivo on a variety of plants demonstrated that GDH operates in the direction of glutamic acid deamination Robinson *et al.* (1992); Aubert *et al.* (2001). It was concluded that GDH is involved in the supply of 2-oxoglutarate rather than in the assimilation of ammonium when carbon becomes limiting (Robinson *et al.* (1992); Aubert *et al.* (2001); Miflin and Habash (2002). The physiological role of GDH in the whole-plant context remains speculative given the recent finding that the majority of the GDH protein is located in the mitochondria of companion cells Dubois *et al.* (2003). GDH was increased in the mitochondria and appeared in the cytosol of companion cells. Taken together, our results suggest that the enzyme plays a dual role in companion cells, either in the mitochondria when mineral nitrogen availability is low or in the cytosol when ammonium concentration increases above a certain threshold Tercé-Laforgue *et al.* (2004). Inhibition of NADH-GDH by arsenate in excised bean leaf segment Jot and Gadre, (1995). Ammonia in higher plants is believed to be assimilated primarily by the glutamine synthetase–glutamate pathway Miflin and Lea (1980). The GDH enzyme could operate primarily in the assimilation or reassimilation of ammonium and play a complementary role to the GOGAT cycle Srivastava and Singh (1987). Two isozymic forms of GOGAT (i.e., Fd-GOGAT and NAD (P) H-GOGAT) are of common occurrence in the tissues of higher plants and are involved in the assimilation of primary ammonia as well as of photo-respiratory ammonia Miflin and Lea (1980). The GS and GOGAT cyclic mechanism is largely active when exogenous nitrogen concentrations are limiting, due to the high affinity of GS for ammonium. This pathway utilizes approximately 15% of the cells' adenosine triphosphate (ATP) requirement Reitzer (2003) for the production of glutamine and its activity is, therefore, strictly regulated at both transcriptional and posttranslational levels in order to prevent energy wastage. Thus, the enzyme seems to be playing a pivotal role in linking the enzyme

activity in plants, but the effect seems to be dependent on the isoform and the plant species analyzed Puranik and Srivastava (1994).

10. Defense mechanisms against negative effects of mercury

Plants have developed defense mechanisms that ensure tolerance characteristics to cope with the negative effect of toxic metals or metalloids. These mechanisms include chelation, compartmentalization, biotransformation, and cellular repair Salt *et al.* (1998). Ajsuvakova *et al.* (2020) stated that present study addresses existing data on the affinity and conjugation of sulfhydryl (thiol; -SH) groups of low- and high-molecular-weight biological ligands with mercury (Hg) Fig. (34).

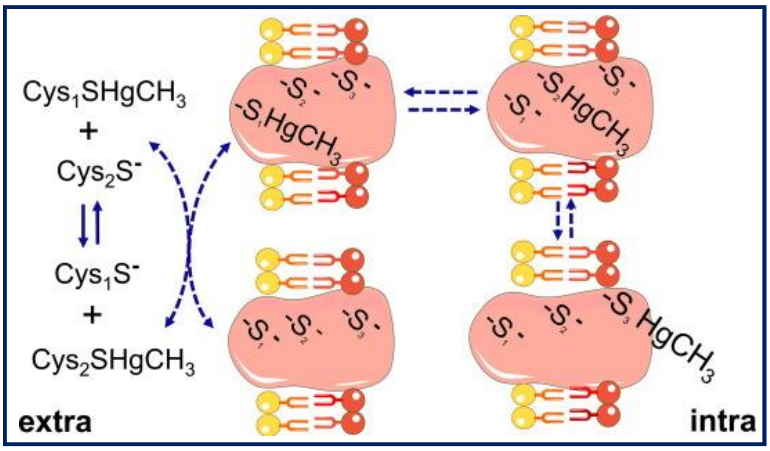

Fig. 34: Illustrates sulfhydryl groups as targets of mercury toxicity. After: Ajsuvakova *et al.* (2020)

The consequences of these interactions with special emphasis on pathways of Hg toxicity are highlighted. Cysteine (Cys) is considered the primary target of Hg, and link its sensitivity with thiol groups and cellular damage. *In vivo*, Hg complexes play a key role in Hg metabolism. Due to the increased affinity of Hg to SH group in Cys residues, glutathione (GSH) is reactive. The geometry of Hg (II) glutathione's is less understood than that with Cys. Both Cys and GSH Hg-conjugates are important in Hg transport. The binding of Hg to Cys mediates multiple toxic effects of Hg, especially inhibitory effects on enzymes and other proteins that contain free Cys residues. In blood plasma, albumin is the main Hg-binding (Hg^{2+}, CH_3Hg^+, $C_2H_5Hg^+$, $C_6H_5Hg^+$) protein. At the Cys_{34} residue, Hg^{2+} binds to albumin, whereas other metals likely are bound at the N-terminal site and multi-metal binding sites. In addition to albumin, Hg binds to multiple Cys-containing enzymes (including manganese-superoxide dismutase (Mn-SOD), arginase I, sorbitol dehydrogenase, and δ-aminolevulinate dehydratase, etc.) involved in multiple processes. The affinity of Hg for thiol groups may also underlie the pathways of Hg toxicity; in particular, Hg-SH may contribute to apoptosis modulation by interfering with Akt/CREB, Keap1/Nrf2, NF-κB, and mitochondrial pathways. The toxicity of inorganic Hg forms (e.g., $HgCl_2$) is at least in part explained by the element's great affinity for biomolecules containing SH groups Phytochelatins (PCs) are cysteine-rich polypeptides of general structure [y(-Glu-Cys)$_2$-11-Gly], which play an essential role in the detoxification of some heavy metals (cadmium (Cd), copper (Cu), zinc (Zn), mercury (Hg), and lead (Pb) and metalloids (arsenic) in fungi, plants, nematodes, and other organisms (Grill *et al.* (1987); Clemens *et al.* (1999); Cobbett and Goldsbrough (2002); Vivares *et al.* (2005). The inhibitory effect of heavy metals may be due to the (**a**) Blocking of the supply of reducing equivalents of nitrate reduction, (**b**) Formation of mercurial derivatives of –SH of NR, and
(**c**) Synthesis of PCs Subhadra and Sharma, (2007).

The strength of mercury (II) binding to GSH and PC follows the given order: Y Glu-Cys-Gly(y Glu-Cys)$_2$ Gly(y Glu-Cys)$_3$ Gly(y Glu- Cys)$_4$ Gly Patra and Sharma (2000). The transport of both PCs and Cd as its peptide complex, from the cytoplasm into the vacuole Saltz and Rauser (1995). In a second detoxification step, the PC–heavy metal complex is transported to the vacuole. An (ATP-binding

cassette)- ABC transporter, Hmt1, accepting low-molecular-weight PC–heavy metal complexes as substrate, has been identified in *Schizosaccharomyces pombe* Ortiz *et al.* (1995), and phytochelatins (PCn) an MgATP-dependent transport activity for PC3 and PC3 ± Cd complexes has also been demonstrated in plants Salt and Rauser, (1995). The high stability of the PC-Hg multi complexes (mPC-nHg) seems to be the main reason for the lack of previous Hg-PC characterization studies. A modified method to detect and quantify unbound PC of Hg in plant extracts via high-performance liquid chromatography coupled to electrospray tandem mass spectrometry and inductively coupled plasma mass spectrometry in parallel. Iglesia-Turin (2006) separated PC from Hg by adding the chelating agent sodium 2, 3-dimercaptopropanesulfonate monohydrate. PC2 was observed in plant samples. The best activator tested was Cd followed by Ag, Bi, Pb, Zn, Cu, Hg, and Au cations; these metals also induce PC biosynthesis in vivo in plant cell cultures Cobbett (2000). Mercury inactivates the GSH enzyme by binding to the thiol (–SH) groups of protein. In addition, it also provides evidence that GSH serve as a precursor for PC, and this was confirmed by using Buthionine sulphoximine (BSO), an inhibitor of γ-glutamyl- cystein synthethase and a key enzyme of synthesis pathway (Jot and Subhadra 2010). Studies employing the GSH biosynthetic inhibitor, buthionine sulfoximine, suggested an increase in the level of PCs and maintenance of GSH homeostasis in transgenic plants during exposure to excess zinc as the possible mechanism behind this tolerance Singla-Pareek *et al.* (2006). PC plays a key role in protecting macromolecules from damage by free radicals by trapping them in an aqueous phase Freedman *et al*. (1989). When the non-PC-based mechanism of detoxification gets exhausted and free metal ions become available to induce PC synthesis Schat et al., (2002). Exposure to excess Cu is capable of stress induction, in which the role of oxidative stress and reactive oxygen species (ROS) production may be involved (Stadtman and Oliver (1991), Waldermar *et al.* (1994). On the other hand, under Cu toxicity, excess copper is an efficient generator of ROS in Fenton-type reactions, leading to disturbances in metabolic pathways and macromolecule damages Hegedus *et al.* (2001). The oxidative stress is bound up with the increased metal accumulation in plants and decreased efficiency of the ascorbate–GSH cycle under the metal stress Wang *et al.* (2009). Exposure to toxic metals also induces plants to accumulate high amounts of proline Štefl and Vaš kov (1982). Increased accumulation of proline leads to the increase of glutamate kinase activity and creates a possibility for an increase in glutamic acid content due to the synthesis of GSH and PCs in plant cells Pavl kov *et al.*, (2007). An increase of free proline inhibits biosynthesis of its excessive amounts in plants under heavy metal excess, and these results in the preferred utilization of glutamate for the metabolic route leading to PC synthesis Pavl kov *et al.* (2008).

11. Role of selenium for mercury detoxification in soil–plant systems

Pařízek and Oštádalová (1967) first noted the protective effect of Se against Hg toxicity over 50 years ago in rats; most of the early studies were in mammals. Thi *et al.* (2021) reported that feasible countermeasures to mitigate mercury (Hg) accumulation and its deleterious effects on crops are urgently needed worldwide. Selenium (Se) fertilizer application is a cost-effective strategy to reduce mercury concentrations, promote agro- environmental sustainability and food safety, and decrease the public health risk posed by Hg-contaminated soils and its accumulation in food crops. This holistic review focuses on the processes and detoxification mechanisms of Hg in whole soil–plant systems after Se application. The reduction of Hg bioavailability in soil, the formation of inert HgSe or/and HgSe containing proteinaceous complexes in the rhizosphere and/or roots, and the reduction of plant root uptake and translocation of Hg in plant after Se application are systemically discussed. In addition, the positive responses in plant physiological and biochemical processes to Se application under Hg stress are presented to show the possible mechanisms for protecting the plant. However, application of high levels Se showed synergistic toxic effect with Hg and inhibited plant growth. The effectiveness of Se application methods, rates, and species on Hg detoxification is compared, this provides a good approach for plant production in Hg-contaminated areas to meet food security demands and reduce the public health risk Fig. (35).

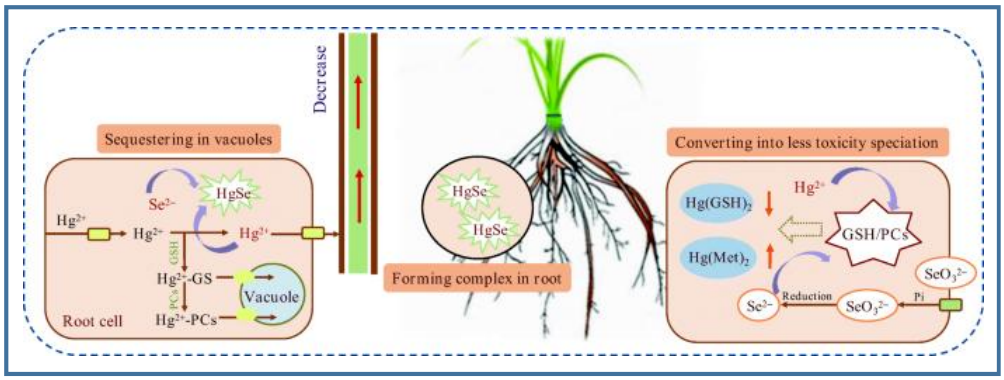

Fig. 35: Illustrates reducing Hg accumulation and toxicity within plant. After: Thi *et al.* (2021)

Several studies demonstrated that Se application could reduce the toxicity of many heavy metals, including Hg, Cd, and Pb, through the reduction of heavy metal accumulation by plants Mukherjee and Sharma (1988); Shanker *et al.* (1996a); Thangavel *et al.* (1999). The protective effect involved the binding of Se to Hg, thereby, acting as a "tonic" that sequestered Hg in a form that no longer harmed important biomolecules. To understand how Se protects against Hg toxicity, it is necessary to understand the interaction processes between Hg and Se in the soil.

Speciation of Hg in soil , most common forms of Hg in soils include elemental mercury (Hg0),mercuric mercury (Hg^{2+}), mercuric sulfide (HgS), and methyl Hg (CH_3Hg^+) Clarkson and Magos (2006); Yang *et al.* (2008). Hg^{2+} is the dominant and highly soluble Hg species under the highly oxidizing conditions of unflooded soils Fernandez-Martinez *et al.* (2015). Mercury is reduced in the soil environment, as follows: Hg0 ⇆ 2Hg $^{2+}$ ⇆ Hg^{2+} ⇆ (CH_3) Hg ⇆ (CH_3)2Hg Shanker *et al.* (1996b), McNear *et al.* (2012). Bacterial merB (organ mercurial lyase) facilitates the protonolysis of organic-Hg to Hg^{2+}, whereas bacterial merA (mercuric ion reductase) transforms Hg^{2+} to Hg0 Ruiz and Daniell (2009). Luis *et al.* (2011) reported that in bacteria, mercury resistance mer genes are generally organized in operons located on plasmids and transposons Yurieva *et al.* (1997), Silver and Phung (2005). The narrow-spectrum mercury resistance mer RTPADE operon confers resistance to inorganic mercury and the broad-spectrum mercury resistance mer RTPAGBDE operon confers resistance to inorganic and organic mercury species Fig. (36).

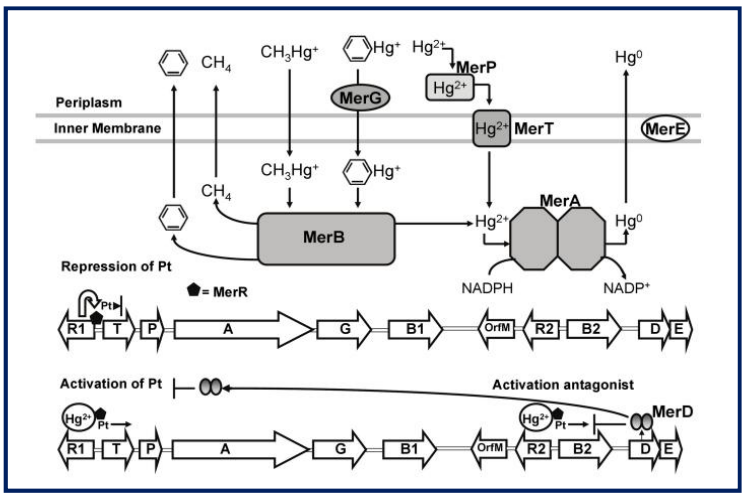

Fig. 36. Illustrates bacterial mechanisms for organic and inorganic mercury detoxification and regulation of the mer genes. MerA, mercuric reductase; MerB, organomercurial lyase; MerP, periplasmic mercury-binding protein; MerT, membrane mercury transport protein; MerG, periplasmic protein involved in cell permeability to phenylmercury; MerE membrane protein that probably acts as a broad mercury transporter; MerR, transcriptional activator or repressor of the transcription of mer genes (black pentagon); MerD, co-represor of transcriptional activation; Pt, promoter of merT and merB2 genes. After: Luis *et al*. (2011)

The bacterial mechanism of mercury resistance includes the uptake and transport of Hg^{2+} by the periplasmic protein MerP and the inner membrane protein MerT. MerE is a membrane protein that probably acts as a broad mercury transporter mediating the transport of both methyl mercury and Hg^{2+} Kiyono *et al*. (2009). The cytosolic mercuric reductase MerA reduces Hg^{2+} to less toxic elemental mercury Barkay *et al*. (2003).The gene merB encodes an organomercurial lyase that catalyses the protonolytic cleavage of carbon-mercury bonds Moore *et al*. (1990), Misra (1992) . The mer G gene product is involved in the reduction of cellular permeability to organomercurial compounds Kiyono and Pan-Hou (1999). MerD probably acts as a distal co-repressor of transcriptional activation Barkay etal (2003), Champier etal (2004). MerR is the activator or repressor of the transcription of mer genes in presence or absence of mercury ions, respectively Ni'Bhriain etal (1983), Permina etal (2006). At mercury stress condition the transcriptional activator MerR triggers the expression of the structural mer genes Brown etal (2003). Sequencing of the native IncP-1b plasmid pTP6 that was originally isolated from mercury-polluted river sediment in a triparental mating showed that all these genes are part of transposon Tn50580 Smalla etal (2006). The heavy metal-resistant model bacterium *Cupriavidus metallidurans* strain CH34 harbors two large plasmids, pMOL28 and pMOL30, which carry genetic determinants for heavy metal resistance Mergeay etal (2003). Each plasmid contains a mer RTPADE operon that confers a narrow-spectrum mercury resistance. To improve inorganic and organic mercury resistance of strain C. metallidurans CH34, the IncP-1b plasmid pTP6 was introduced into strain CH34 in this study. The trans conjugant strain *Cupriavidus metallidurans* MSR33 showed a broad-spectrum mercury resistance and was able stop efficiently remove mercury from polluted water.

Mercuric chloride and mercuric hydroxide are likely to be reduced to Hg0 as follows: $Hg^{2+} + Cl_2$ and $Hg^{2+} + [OH]_2$ into Hg0) Shanker *et al*. (1996b), McNear *et al*. (2012). The speciation of Se in soil Selenium exists in different forms in the soil, including selenate (SeO_4^{2-}), selenite (SeO_3^{2-}), elemental Se (Se0), and selenide (Se^{2-}) Zhang *et al*. (2014). Se0 and Se^{2-} have poor mobility Tolu *et al*. (2011), SeO_3^{2-} and SeO_4^{2-} are both highly available for plant uptake, whereas SeO_3^{2-} is less available than $SeO4^{2-}$ due to its strong adsorption onto soil particles Nakamaru and Altansuvd (2014). Long periods of overlying water stimulate lower pH values and anoxic conditions in flooded paddy soil Rothenberg and Feng (2 012). Under anoxic conditions, SeO_4^{2-} can be reduced to SeO_3^{2-} and then rapidly transformed into SeO and even to Se^{2-} or organic Se by sulfate-reducing bacteria (SRB) as follows: $SeO_4^{2-} \rightarrow SeO_3^{2-} \rightarrow SeO \rightarrow Se^{2-}$ (Yang *et al*. 2008; Li *et al*. (2014a).

11.1. Reduction of Hg availability on the interface of soil–plant root after Se application

Besides decreases of Hg bioavailability in soil after Se application, decline of Hg availability on the interface of soil–plant root also was identified by directly tracking inert HgSe or/and HgSe-containing proteinaceous complexes in the roots. These complexes reduced Hg accumulation in plants by inhibiting Hg uptake and transport. Hasanuzzaman *et al*. (2011) reported that selenium (Se) supplementation could restrict metal uptake by roots and translocation to shoots, which is one of the vital stress tolerance mechanisms. Selenium can also enhance cellular functions like membrane stability, mineral nutrition homeostasis, antioxidant response, photosynthesis, and thus improve plant growth and development under metal/metalloid stress. Metal/metalloid toxicity decreases crop productivity and uptake of metal/metalloid through food chain causes health hazards. Selenium has been recognized as an element essential for the functioning of the human physiology and is a beneficial element for plants. Low concentrations of Se can mitigate metal/metalloid toxicity in plants and improve tolerance in various ways Fig. (37).

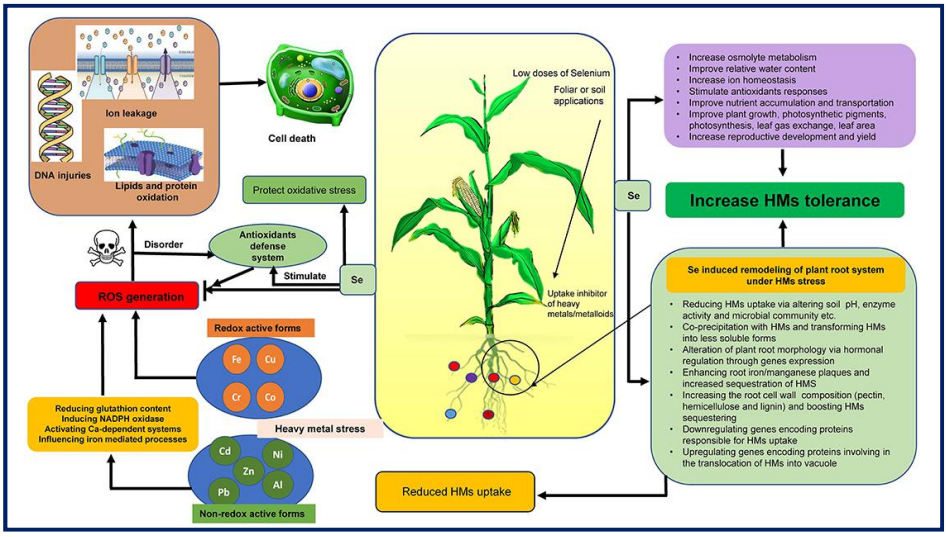

Fig. 37: Illustrates ROS generation under heavy metal stress and protective roles of selenium. After: Hasanuzzaman *et al*. (2011)

Selenium stimulates the biosynthesis of hormones for remodeling the root architecture that decreases metal uptake. Growth enhancing function of Se has been reported in a number of studies, which is the outcome of improvement of various physiological features. Photosynthesis has been improved by Se supplementation under metal/metalloid stress due to the prevention of pigment destruction, sustained enzymatic activity, improved stomatal function, and photosystem activity. By modulating the antioxidant defense system Se mitigates oxidative stress. Selenium improves the yield and quality of plants. However, excessive concentration of Se exerts toxic effects on plants.

In addition, the restriction of Hg access into the root of plants, due to the promotion of the formation of Fe plaques outside plant roots after Se application, may also be important for reducing the accumulation of Hg in roots and shoots. Reduction of Hg availability by formation of insoluble HgSe precipitate in root formation of insoluble HgSe precipitate in root formation of inert insoluble HgSe precipitate. The formation of HgSe insoluble complexes within plants cannot be completely ruled out, although HgSe insoluble precipitate likely dominates in the soil. Hypothetical pathways for Hg uptake in plants involve cellular entry through ionic channels and competition with the closest chemical relatives of essential metals for Hg^{2+} transporters Blazka and Shaikh (1992); Clemens (2006). Hg^{2+} and CH_3Hg^+ are the principal chemical forms of Hg taken up by roots from the soil Clemens (2013), and Hg^{2+} accumulates in roots Meng *et al*. (2014); Zhao *et al*. (2014). Selenium is primarily taken up from the soil by plants as SeO_4^{2-} or SeO_3^{2-} Zhu *et al*. (2009). After absorption by the plant root, SeO_4^{2-} is reduced to SeO_3^{2-}, reacts with glutathione (GSH), and is reduced to Se^{2-} in the rhizosphere Zhu *et al*. (2009); Han *et al*. (2015). The combination of Se2− with Hg^{2+} forms the HgSe complexes in roots, as follows: Hg0 + Se0 → HgSe and/or Hg^{2+} + Se^{2-} → HgSe, which may drastically increase the accumulation of Hg in roots Zhang *et al*. (2012), Li *et al*. (2015) Fig. (38). Under flooded soil conditions, over 90% of Hg was restricted to rice roots after SeO_3^{2-} application of 0.01−0.5 µg/ mL in Hg-contaminated soil, and 27.8% of Hg was present as the HgSe complex Li *et al*. (2015). Zhao *et al*. (2013) analyzed the speciation of Hg (with Hg L3-edge XANES) in garlic (*Allium sativum L*.) tissues under hydroponic solution conditions, and they concluded that the direct binding of Se and Hg as HgSe only occurs in roots (CH_3Hg+ with selenol-containing biomolecules. Compared with thiols, binding between Hg and selenols was stronger. Therefore, Hg^{2+} and CH_3Hg+ complexes with selenols were more stable than their thiol analogs, thereby showing Hg–Se antagonism, resulting in the effective reduction of Hg^{2+} and CH_3Hg+ in plant with the addition of Se into the soil Wang *et al*. (2014); Zhang *et al*. (2012). Size exclusion chromatography and proteolysis revealed that water-soluble Hg was localized in the roots in association with Se in the form of a high molecular weight entity, which was difficult to be translocated and metabolized. Yathavakilla and Caruso (2007) found that water-soluble

Hg associated with Se and formed a high molecular weight (>600 kDa) proteinaceous complex in the roots of soybean (*Glycine max* L.) grown in soil containing both Hg and Se

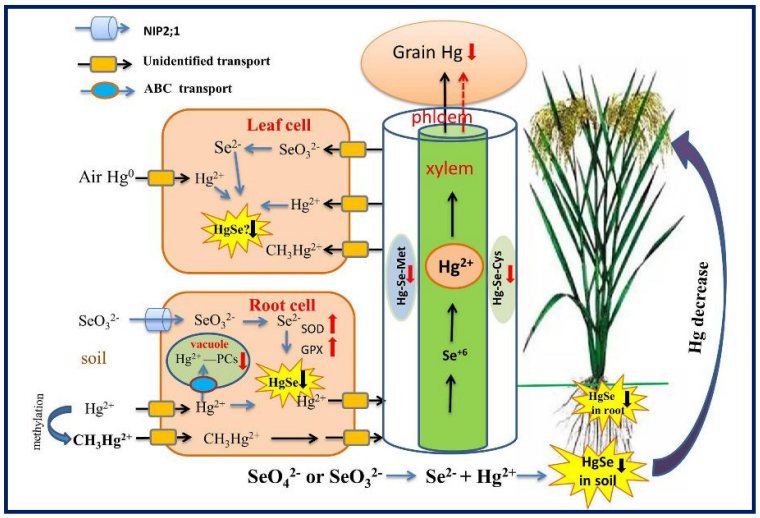

Fig. 38: Illustrates flow diagram representing the transporters involved in the uptake, translocation, and accumulation of different selenium species through xylem and phloem to the grain. The main transporters involved in inorganic Se uptake by plants (SULTR1;1, SULTR1;2 for selenate, NIP2;1, PT2 and PT8 for selenite, AA Tr. For amino acids). Organic Se forms are transported into the xylem via amino acid permeases (AA Tr.) and delivered to the shoots. Selenate is the major Se species present in the xylem and loaded into the xylem by SULTR2;1. Organic-Se compounds are transported into the seed via the phloem, while selenate is transported via both xylem and phloem. The translocation of SeMet to the seeds is enhanced by overexpression of the NRT1;1B transporter. After: Zhou *et al*. (2020)

Mounicou *et al*. (2006) found a high molecular weight (>70 kDa) compound containing Se and Hg in the root extract of Indian mustard (*Brassica juncea* L. Czern.) grown in hydroponics. This compound was associated with either a polysaccharide or a protein. Afton and Caruso (2009) identified a possible Se–Hg association in a plant-root protein in green onion (*Allium fistulosum* L.) grown in perlite media by applying size exclusion and capillary-reversed phase chromatography coupled with inductively coupled plasma mass spectrometry (ICPMS). McNear *et al*. (2012) used capillary-reversed phase chromatography coupled with ICPMS, µ-XANES, and micro-synchrotron X-ray fluorescence and found that Hg may bind to –SH groups of the cell wall or plasma membrane proteins in green onion roots and may react with reduced Se^{2-} to form HgSe–BSS complex. However, Se^{2-} reacted with an abundant amount of free Hg^{2+} to form a solid HgSe precipitate outside the root in the perlite media. HgSe–BSS comprised an Hg^{2+} and Se^{2-} core to which GSH was appended via a Se–S or Hg–S bond McNear *et al*. (2012). Compared with Hg-containing proteins with small molecular weights, the formation of Hg-Se-containing proteins with high molecular weights can more effectively inhibit the translocation of CH_3Hg^+ to the aboveground parts of rice plants. Wang *et al*. (2016a) also proposed that a CH_3Hg^+ –Se interaction could exist within rice roots through the formation of CH_3Hg^+ –Se complexes, when CH_3Hg^+ distribution in roots was enhanced under the SeO_3^{-2} and SeO_4^{-2} fertilization. They concluded that CH_3Hg^+ –Se antagonism within plants was likely sufficient to induce such a reduction Wang *et al*. (2016a). Zhao *et al*. (2014) reported that rice cultured in Hg- and/or Se-contaminated fields is an important food source of human Hg/Se intake. There are elevated Hg and Se levels in the soil of the Wanshan District, Guizhou Province. Here we attempted to explore how a Hg antagonist, Se, modulates the absorption and accumulation of inorganic mercury (IHg) and methyl mercury (MeHg) in rice. They stated inorganic mercury (IHg) mainly accumulated in the rice roots, but some also accumulated in the rice grain. In comparison to IHg, MeHg can be concentrated in the rice grain, and the proportion of MeHg in the rice grain may account for above 40% of the total Hg. Selenium can protect against Hg phytotoxicity in rice and inhibit IHg accumulation in rice tissues, but was not

remarkable for MeHg at a low dosage exposure level in this study. These discrepancies imply mechanistic differences between IHg and MeHg absorption and accumulation in rice. They reported that Se plays an important role in modulating Hg uptake, transportation and accumulation in rice and considering being a naturally existing element that effectively reduces Hg accumulation in rice, which may have significant implications for food safety

Zhao *et al*. (2014) stated that SRXRF technique is a powerful tool for non-destructive elemental analysis with exceptional sensitivity Gao *et al*. (2008).To reveal the influence of Se treatment on Hg micro-zone distribution in rice grown up in Hg-contaminated soil with or without Se treatment, 2D elemental distribution of the roots, leaves and rice grains were imaged using micro-SRXRF. The normalized X-ray fluorescence intensities are scaled from blue (minimum) to red (maximum). These images visually demonstrate the distributions and accumulations of Hg and Se in rice. The results are shown in Fig. (39-a1) shows that Hg was mainly localized in the epidermis and the pericycle of the rice root.

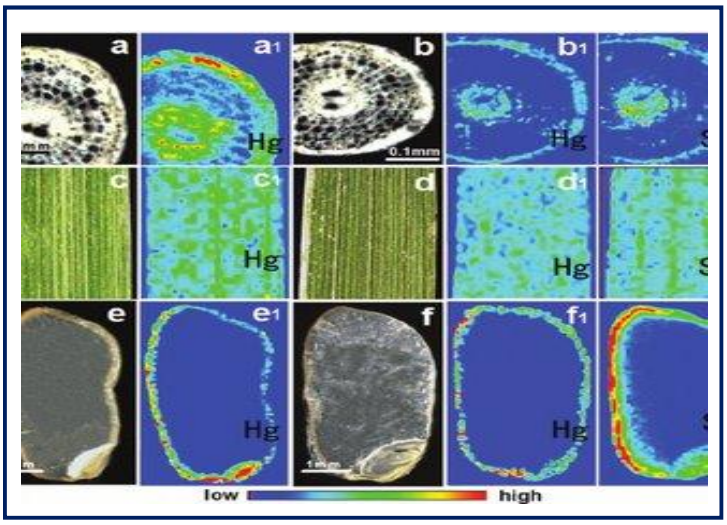

Fig. 39: The distribution of Hg and Se in different tissues of the paddy soil cultured rice measured by m-SRXRF. (a) The cross section of the root tip from rice under Hg exposure (a1, Hg XRF image); (b) the cross section of the root tip from rice under Hg and Se exposure (b1, Hg XRF image; b2, Se XRF image); (c) the leaf from Hg exposed rice; (d) the leaf from Hg and Se co-exposed rice; (e) the rice grain from Hg exposed rice; (f) the rice grain from Hg and Se co-exposed rice. After: Zhao *et al*. (2014)

Due to the high affinity of Hg for the sulfhydryl groups in the surface of the root, Cheeseman *et al*. (1988), Carrasco-Gil *et al*. (2011) Hg can be enriched to quite a high concentration in the epidermis of the rice roots. Moreover, Hg can also be accumulated in the vessel of the roots, implying that Hg is able to penetrate the root surface into the vascular cylinder and then transport upwards. For Se/Hg co-exposed rice, one can see that the distribution of Se correlates well with that of Hg in the rice roots Fig. (39-b1, b2), and both of them principally concentrate in the epidermis and pericycle of the rice root. Comparing Fig. 39-b1 with a1, a substantial decrease in Hg accumulation in the epidermis and stele of the rice root can be found. This is consistent with the ICP-MS results shown in Fig. (39). The correlation between Hg and Se distribution in rice roots, combined with the strong affinity of Se to Hg, suggests that Hg and Se may form an Hg–Se complex in the rice root. This may explain how Se addition could inhibit Hg uptake and translocation in rice. Shanker *et al*. have reported the existence of an Hg–Se compound in the rhizosphere of radish, which can block the absorption of Hg through the root Shanker *et al*. (1996). Caruso *et al*. (2011) have confirmed the existence of an Hg–Se compound in the roots of Brassica juncea and soybean. Mounicou *et al*. (2006), Yathavakilla and Caruso (2007) Fig. (39) c1, d1 and d2 show the effect of Se on Hg distribution in rice leaves. It can be seen that Hg is dispersed over the leaves, and some is specially located in the leaf vein Fig. (39 - c1). Furthermore, the Se

distribution pattern correlates well with that of Hg in the rice leaves Fig. (39-d2). The content of Hg in the leaves collected from the Hg/Se co-exposed rice plant Fig. (39-d1) is much less than that of the Hg exposed group Fig. (39-c1), indicating the inhibitive effect of Se on Hg transportation from the roots to the leaves through the vascular cylinder. The effects of Se on the distribution and accumulation of Hg in the rice grain are illustrated in Fig. (39- e1, f1 and f2). From Fig. (39- e1), it is shown that Hg is principally concentrated on the surface of the rice grain (the aleurone layer), especially along the growth site of the embryo. It is notable that a considerable amount of Hg can accumulate in the embryo part Fig. (39-e1), while less Hg is located in the rice endosperm. Fig. (39-f1 and f2) show the distributions of Hg and Se in rice grain collected from Hg/Se co-exposed rice. Except for the location in the aleurone layer like Hg, a considerable proportion of Se can penetrate into the endosperm of the rice grain. Moreover, Se distribution in the embryo is more extensive than that of Hg.

A similar Se distribution pattern was previously reported, Williams *et al*. (2009) in which much Se accumulation in the outer regions of the rice grain was observed, and an amount of Se was concentrated in the chalazal zone that shares a close proximity to the ocular vascular trace. Comparing Fig. (39-f1) with Fig. (39-e1), the concentration of Hg in the embryo part of the rice grain from Se and Hg co-exposed rice is much lower than that of the rice exposed to Hg alone. This indicates that Se can interfere with Hg accumulation in the rice grain, and suggests that Se treatment may mitigate Hg toxicity towards the growth and development of rice seeds, as the embryo is the budding point of the rice seed. In addition, the essential elements (Fe, Cu, Zn, K, Ca etc.) are mainly concentrated in the embryo of the rice grain. Suggesting that the necessary nutrient elements, rather than the toxic elements, can be selectively accumulated in the rice grain. Furthermore, it implies the existence of a preventive mechanism for toxic element accumulation in rice. In conclusion, Se treatment can inhibit Hg uptake and transportation from the rice root to the aerial part, which finally results in lower Hg accumulation in the rice grain, especially, in the aleurone layer and embryo. The effect of Se on MeHg is less remarkable than IHg, along with the discrepancy of IHg and MeHg accumulation in different rice tissues indicating mechanistic differences in the absorption and transportation of IHg and MeHg in rice. The present study may provide valuable information for sequestering Hg and novel insights for addressing food safety in Hg/Se polluted environments. More researches on the positions for the methylation of IHg in vitro or in vivo and the phyto-biological behaviors of IHg and MeHg in rice will be needed to further understand the ecological toxicology of this toxic element.

12. Molecular response to Hg

Genome-wide transcriptome analysis has become a powerful tool to identify a set of genes that are specifically regulated by heavy metals Becher *et al*. (2004); Weber *et al*. (2004); Herbette *et al*. (2006); Van de Mortel *et al*. 2008; Gorfer *et al*. 2009; Yamaguchi *et al*. (2010); Ding *et al*. (2011). Suppression subtractive hybridization (SSH) is a widely used method for separating DNA molecules that distinguish two closely related DNA samples. Two of the main SSH applications are cDNA subtraction and genomic DNA subtraction. In fact, SSH is one of the most powerful and popular methods for generatingsubtracted cDNA or genomic DNA libraries. The SSH method is based on a suppression PCR effect and combines normalization and subtraction in a single procedure. The normalization step equalizes the abundance of DNA fragments within the target population, and the subtraction step excludes sequences that are common to the populations being compared. This dramatically increases the probability of obtaining low-abundance differentially expressed cDNA or genomic DNA fragments, and simplifies analysis of the subtracted library. In our hands, the SSH technique has enriched over 1000-fold for rare sequences in a single round of subtractive hybridization. Using suppression subtractive hybridization (SSH) Fig (40), six genes (PsSAMT, PsI20H, PsNDA, PsAPSR, PsPOD, PsHMIP6B) were identified and strongly regulated by Hg in roots of pea (Pisum sativum) Sa¨venstrand and Strid (2004). Sahebi *et al*. (2015) reported that Suppression subtractive hybridization (SSH) is an effective method to identify different genes with different expression levels involved in a variety of biological processes. This method has often been used to study molecular mechanisms of plants in complex relationships with different pathogens and a variety of biotic stresses.

Compared to other techniques used in gene expression profiling, SSH needs relatively smaller amounts of the initial materials, with lower costs, and fewer false positives present within the results. Extraction of total RNA from plant species rich in phenolic compounds, carbohydrates, and polysaccharides that easily bind to nucleic acids through cellular mechanisms is difficult and needs to

be considered. Remarkable advancement has been achieved in the next-generation sequencing (NGS) field. Because of progress within fields related to molecular chemistry and biology as well as specialized engineering, parallelization in the sequencing reaction has exceptionally enhanced the overall read number of generated sequences per run. Currently available sequencing platforms support an earlier unparalleled view directly into complex mixes associated with RNA in addition to DNA samples. NGS technology has demonstrated the ability to sequence DNA with remarkable swiftness, therefore allowing previously unthinkable scientific accomplishments along with novel biological purposes. However, the massive amounts of data generated by NGS impose a substantial challenge with regard to data safekeeping and analysis. In addition examines some simple but vital points involved in preparing the initial material for SSH and introduces this method as well as its associated applications to detect different novel genes from different plant species.

Moreover, evaluates general concepts, basic applications, plus the probable results of NGS technology in genomics, with unique mention of feasible potential tools as well as bioinformatics Fig. (40). They also stated that suppression subtractive hybridization involves five main steps: **(1)** isolation of total messenger RNA (mRNA), followed by the synthesis of double-stranded cDNA fragments for both the driver and tester samples; **(2)** digestion of double-stranded cDNA fragments from the previous step; **(3)** ligation of two different tester cDNA aliquots with two different adaptors A and B provided in the kit Fig. (40-I). Adobe Photoshop CS5 and Illustrator CS6 software were used to prepare images showing the whole process involved in SSH; **(4)** the first suppressive hybridization at the first hybridization step, an excess of the driver cDNA from sample (A) is added to each sample of tester cDNA (B), then both samples B are heated, denatured, and annealed, generating four different types molecule a, b, c, and d Fig.(40-II); and **(5)** the second suppressive hybridization at the second hybridization step, two hybridized samples are combined and annealed again with a fresh sample of the denatured driver. Under these conditions, only the type (a) single-strand tester cDNA remaining from normalization and subtraction processes will be able to re-associate and form type (b), (c), and new hybrids (e) Fig. (40-III). An important feature of this newly hybrid type (e), distinguishes them from the other hybrids. This new hybrid type has two different adaptors (shown in green and red) at their 50 ends. These two different inverted terminal repeats (adaptors) allow for the amplification of subtracted, normalized cDNA fragments (double-stranded) using PCR and two primers (P1 and P2) provided by the kit. This pair of primers corresponds to the outer parts of the green and red adaptors, respectively, and helps to preferentially amplify cDNA fragments.

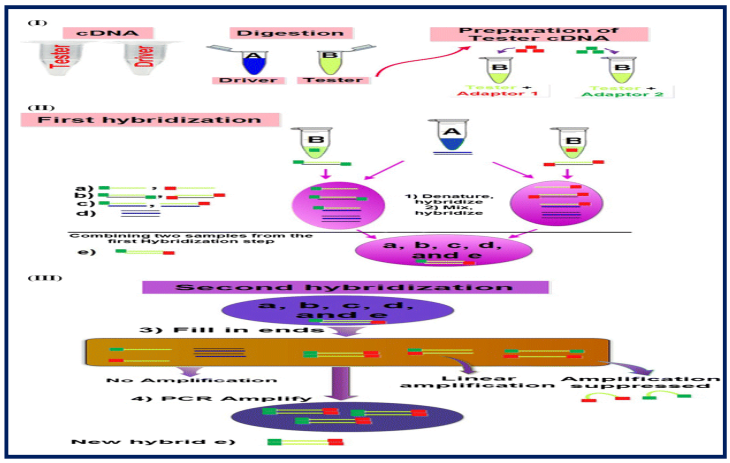

Fig. 40: Illustrates **(I)** Preparation of two-tester cDNA fragments, **(II)**. First hybridization of suppression subtractive hybridization, **(III)**. Second hybridization of suppression subtractive hybridization. After: Sahebi *et al*. (2015)

Some genes induced by Hg are also induced by other heavy metals Yamaguchi *et al*. (2010). Heidenreich *et al*. (2001) profiled the transcriptome of *Arabidopsis thaliana* exposed to Hg^{+2} and found Hg-induced genes encoding proteins involved in chlorophyll synthesis, cell wall metabolism, and P450-mediated biosynthesis of secondary metabolites. Heidenreich *et al*. (2001) they also reported that mercuric-ion-induced gene expression was studied in *Arabidopsis thaliana* Columbia wild type. Rosettes of plants grown for 21 d on agar medium supplemented with 20, 30 and 40 μM $HgCl_2$ were pooled and used to isolate cDNAs of induced genes by suppression subtractive hybridization. Of the 576 clones isolated initially, 31 turned out to be mercury-induced by Northern hybridization. However, kinetic studies using cDNA arrays clearly showed that seven genes were exclusively mercuric-ion-induced, 14 were induced by mercury but also affected by a diurnal rhythm, and 10 clones were only modulated by the day–night cycle. The expression levels of the metal-induced genes increased from 1·5-fold to 10-fold. Functional classification resulted in genes encoding proteins for the photosynthetic apparatus and for the antioxidative system. In addition, unexpected genes, whose connection to mercury ion stress is not evident, were identified. Fig. (41).

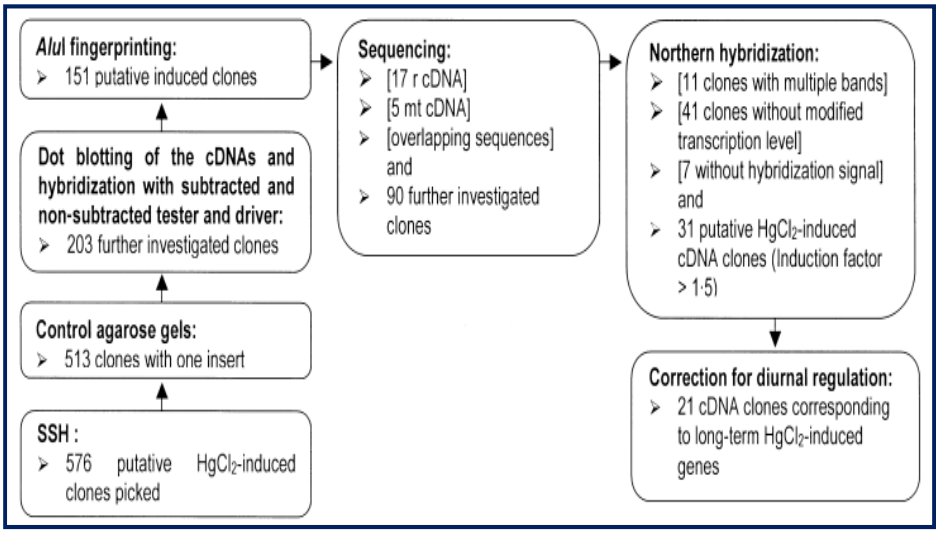

Fig. 41: Illustrates the flow chart showing the procedure used to identify mercuric-ion- induced genes (mt = mitochondrial; r = ribosomal). After: Heidenreich *et al*. (2001)

Two full-length cDNAs coding for a putative metallothionein type 2 protein (SdMT2) and an auxin responsive protein (SdARP) were identified from heavy metal hyperaccumulator *Sesbania drummondii* under Hg exposure; the up-regulated expression of SdARP may contribute to the survival of Sesbania plants with Hg, whereas SdMT2 is likely to be involved in alleviation of Hg toxicity Venkatachalam *et al*. (2009), Christakis *et al*. (2021). Mercury (Hg) is a highly toxic element due to its high affinity for protein sulfhydryl groups, which upon binding, can destabilize protein structure and decrease enzyme activity. Prokaryotes have evolved enzymatic mechanisms to detoxify inorganic Hg and organic Hg (e.g., MeHg) through the activities of mercuric reductase (MerA) and organomercurial lyase (MerB), respectively. Here, the taxonomic distribution and evolution of MerAB was examined in 84,032 archaeal and bacterial genomes, metagenomes assembled genomes, and single-cell genomes. Homologs of MerA and MerB were identified in 7.8 and 2.1% percent of genomes, respectively. MerA was identified in the genomes of 10 archaeal and 28 bacterial phyla previously unknown to code for this functionality.

Likewise, MerB was identified in 2 archaeal and 11 bacterial phyla previously unknown to encode this functionality. Surprisingly, homologs of MerB were identified in a number of genomes (~50% of all MerB-encoding genomes) that did not encode MerA, suggesting alternative mechanisms to detoxify Hg (II) once it is generated in the cytoplasm. Phylogenetic reconstruction of MerA place its origin in thermophilic Thermoprotei (Crenarchaeota), consistent with high levels of Hg (II) in geothermal environments, the natural habitat of this archaeal class. MerB appears to have been recruited to the mer

operon relatively recently and likely among a mesophilic ancestor of Euryarchaeota and Thaumarchaeota. This is consistent with the functional dependence of MerB on MerA and the widespread distribution of mesophilic microorganisms that methylate Hg (II) at lower temperature. Collectively, these results expand the taxonomic and ecological distribution of mer-encoded functionalities, and suggest that selection for Hg (II) and MeHg detoxification is dependent not only on the availability and on type of mercury compounds in the environment but also the physiological potential of the microbes who inhabit these environments. The expanded diversity and environmental distribution of MerAB identify new targets to prioritize for future research They also stated that functionalities encoded by the mer operon are the primary mechanisms microbial cells use for Hg resistance and detoxification Silver and Hobman (2007); Lin *et al*., (2011). At its core, the mer operon encodes a homodimeric flavindependent disulfide oxidoreductase, termed mercuric reductase (MerA) that functions to reduce Hg (II) to volatile Hg (0) that can then diffuse out of the cell Boyd and Barkay (2012) Fig. (42).

The operon may also code for organo-mercury lyase (MerB), that catalyzes the protonolytic cleavage of the C-Hg bond in organo-mercury compounds, among them MeHg Boyd and Barkay (2012). This reaction yields a reduced organic moiety, which in the case of MeHg is methane, and Hg (II); the latter is then reduced to Hg (0) through the activity of MerA Boyd and Barkay (2012). In addition to MerAB, mer operons may code for the periplasmic protein MerP, inner membrane spanning proteins MerT, Mer C, MerE, MerF, and MerG that transport Hg (II) to the cytoplasmic MerA reviewed in Boyd and Barkay (2012). mer operons may also code for transcriptional regulators such as the repressor/activator MerR or anti-activator MerD reviewed in Barkay *et al*. (2003); Lin *et al*. (2011). Through the combined demethylation of MeHg by MerB and decreased concentration of Hg (II) in the cytoplasm by its reduction to gaseous Hg (0) via MerA, the mer operon effectively partitions Hg to the gaseous phase, allowing for microbial growth Barkay *et al*. (2003); Boyd and Barkay (2012). In addition, several other genes responsible for Hg tolerance or accumulation have been identified Rugh *et al*. (1998); Hsieh *et al*. (2009); Ruiz *et al*. (2011); Shen *et al*. (2011); Wei *et al*. (2011). Regulation of gene expression can be also achieved at post-transcriptional and translational levels. Recently, the post-transcriptional regulation of genes by a group of microRNAs (miRNAs) represents a newly discovered mechanism for plant development and response to environmental stresses Jones- Rhoades *et al*. (2006); Phillips *et al*. (2007). Zhang etal (2022) reported that MicroRNAs (miRNAs) are a class of non-coding endogenous small RNAs (long 20–24 nucleotides) that negatively regulate eukaryotes gene expression at post-transcriptional level via cleavage or/and translational inhibition of targeting mRNA. Based on the diverse roles of miRNA in regulating eukaryotes gene expression, research on the identification of miRNA target genes has been carried out, and a growing body of research has demonstrated that miRNAs act on target genes and are involved in various biological functions of plants.

It has an important influence on plant growth and development, morphogenesis, and stress response. Recent case studies indicate that miRNAmediated regulation pattern may improve agronomic properties and confer abiotic stress resistance of plants, to ensure sustainable agricultural production) Fig. (42). In this regard, we focus on the recent updates on miRNAs and their targets involved in responding to abiotic stress including low temperature, high temperature, drought, soil salinity, and heavy metals, as well as plant-growing development. In particular, this review highlights the diverse functions of miRNAs on achieving the desirable agronomic traits in important crops. MiRNA-based research lays the foundation for exploring miRNA regulatory mechanism, which aims to provide insights into a potential form of crop improvement and stress resistance breeding.

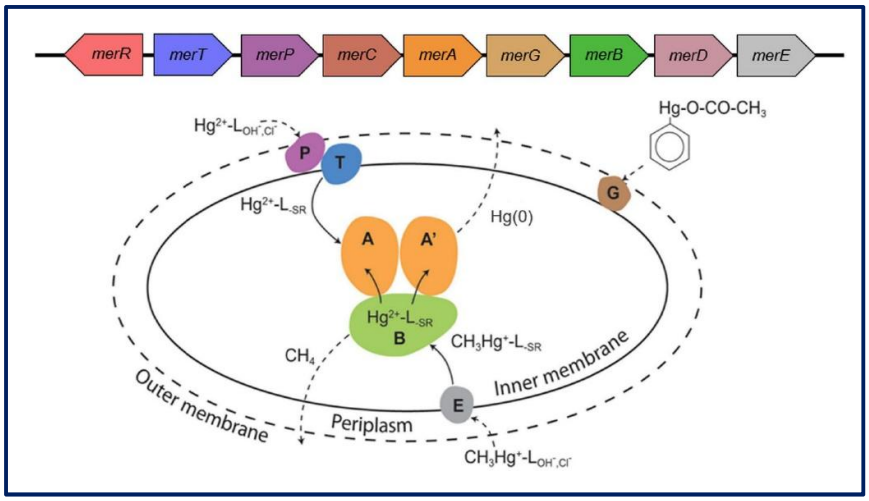

Fig. 42: Illustrates the mer detoxification system. (A) A generic mer operon. (B) The cellular mer-encoded mercury detoxification mechanisms. The outer cell wall is depicted by a broken line illustrating that not all microbes have an outer membrane; broken line arrows depict diffusion; solid line arrows indicate transport or transformations; L = ligand with subscripts denoting the ligand type. The colors of various Mer proteins correspond with the colors of the genes that encode these proteins in panel A. After: Lin *et al*. (2011); Boyd and Barkay (2012) and Christakis *et al*. (2021

miRNAs are processed from single-stranded RNA precursors capable of forming imperfectly complementary hairpin structures by the RNase III enzyme DICER-LIKE1 (DCL1) or DCL4. They are known to base pair their target mRNAs to repress their translation or induce their degradation in organisms Bartel (2004), Li and Mao (2007).

A set of miRNAs in response to Hg stress was first identified from *M. truncatula* Zhou *et al*. (2008a) and *B. napus* Xie *et al*. (2007) using bioinformatic prediction and RT-PCR. With the development of the high-throughput sequencing technology, more novel miRNAs in response to heavy metals have been discovered. More recently, a deep sequencing approach developed by Solexa (Illumina Inc.) has been adopted to investigate global expression and complexity of miRNAs and their targets from *M. truncatula* under Hg Zhou *et al*. (2008a) and Cd Zhou *et al*. (2008b) exposure.

Two small RNA libraries and two degradome libraries were constructed from Hg-treated and Hg-free seedlings of *M. truncatula*, respectively. For miRNAs, each library generated 18.5–18.6 million short sequences, resulting in 10.2–10.8 million clean reads. From this study, at least 52 novel miRNAs with *21 nucleotides were identified from the *M. Truncatula* genome. Statistical analysis on transcript abundance of the new candidate miRNAs revealed that the heavy metal mercury Hg differentially regulated most of them, with 12 miRNAs being specifically induced by Hg exposure. Additionally, they identified 201 individual miRNAs representing 63 known M. truncatula miRNA families, including 12 new conserved and one non-conserved miRNAs that have not been described before. In addition, 130 targets for 58 known (37 conserved and 21 non-conserved) miRNA families and 37 targets for 18 new *M. truncatula*-specific candidate miRNA families were identified by high-throughput degradome sequencing Zhou *et al*. (2008b).

Most of miRNAs target genes coding for tolerance proteins or enzymes. For instance, miR2681 targets several transcripts coding TIR-NBS-LRR disease resistance proteins. Singh *et al*. (2021) reported that the most interesting signaling molecules that regulate a wide array of adaptive stress responses in plants are the micro RNAs (miRNAs) that are a unique class of non-coding RNAs constituting novel mechanisms of post-transcriptional gene regulate on. Recent studies revealed the role of miRNAs in several biotic and abiotic stresses by regulating various phytohormone-signaling pathways as well as by targeting a number of transcription factors (TFs) and defense related genes. Phytohormones are signal molecules modulating the plant growth and developmental processes by regulating gene expression. Studies concerning miRNAs in abiotic stress response also show their vital roles in abiotic stress signaling. Current research indicates that miRNAs may act as possible candidates

to create abiotic stress tolerant crop plants by genetic engineering. Yet, the detailed mechanism governing the dynamic expression networks of miRNAs in response to stress tolerance remains unclear. In this review, we provide recent updates on miRNA-mediated regulation of phytohormones combating various stress and its role in adaptive stress response in crop plants.

They also stated that mode of gene regulation to combat the unavoidable abiotic stress mainly involves the up-regulation or down-regulation of targeted genes Fig. (43).

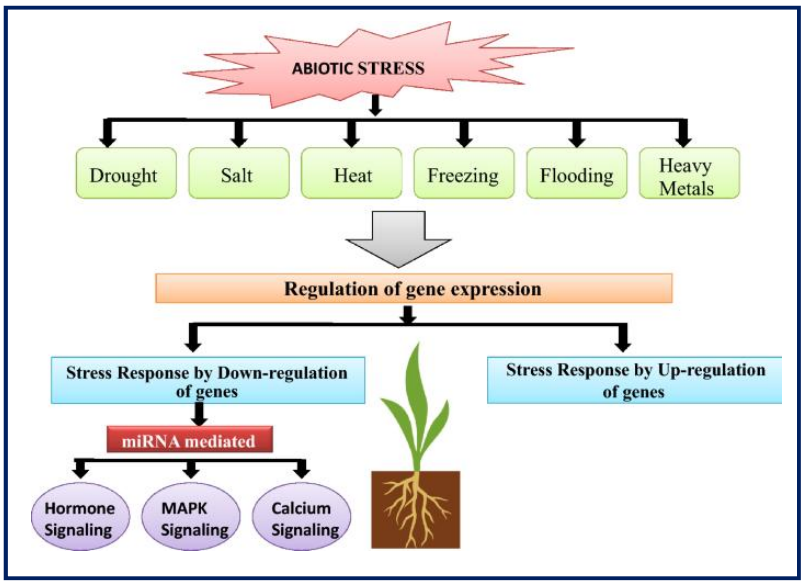

Fig. 43: Illustrates the abiotic stress-mediated gene regulation in plants. This figure depicts miRNA-mediated regulation of gene expression during various abiotic stresses. This positive or negative regulation results in providing stress tolerance to plants by involving MAPK, calcium signaling and phytohormones. After: Singh *et al*. (2021)

The suppression of gene expression happens mainly due to the presence of innumerable tiny soldiers residing within the plant system, which protects them from the extreme conditions. One of these defense system comprises of the members of the 'small RNA world', the micro-RNAs (miRNAs), discovered in the early 1990s which are highly conserved group of non-coding RNA molecules usually 20–24 nucleotides long, functioning via inhibiting translation or cleaving transcripts of targeted genes Lee *et al*. (1993); Wightman *et al*. (1993). The mature miRNAs are produced from primary miRNAs (pri-miRNAs) transcribed from target DNA sequences via RNA polymerase II that mostly down-regulates the mRNAs by binding to its 3' UTR region or sometimes to the 5' UTR region, promoter and coding sequence. Dicer-Like1 (DCL1) recognized the stem loop structured single-stranded RNAs and cuts the pre-imiRNAs forming precursor microRNAs (pre-miRNAs) and subsequently converting it to the miRNAs. These miRNAs are then loaded into the argonaute associated micro-RNA induced silencing complexes (miRISCs) for future processing. The miRNAs tend to be present in the nucleus, nucleolus, mitochondria and endoplasmic reticulum membrane and control the post-transcriptional gene silencing mechanism by commuting through those different sub-cellular components Makarova *et al*. (2016).

The miRNAs are involved for providing abiotic stress tolerance, maintaining nutrient homeostasis and transcriptional regulation of gene expression in plants. Due to a complicated network of action, very few miRNAs have been characterized for their role in abiotic stress but this field is dynamically expanding nowadays with more miRNAs being characterized. Since, one of the major challenges for our world today is "food security" and abiotic stress apparently adds to it by reducing growth and productivity of plant. Thus, a detailed study of the mode of action of miRNAs would be highly beneficial in developing strategies for mitigation of a wide array of abiotic stresses in plants. Various physical and chemical factors such as high soil salinity, drought, fooding, extreme temperatures, ultraviolet (UV) radiation, heavy metal (HM) toxicity and nutrient scarcity collectively comprising the abiotic stress affect plants worldwide Wang *et al*. (2003); Wani *et al*. (2016). In response to the abiotic

stress, several signaling pathways involving various phytohormones are also activated. Although miRNAs and phytohormones have different metabolic and transduction pathways, recent studies suggest interplay in miRNAs pathways and phytohormone responses during a number of abiotic stresses. This interaction results in overcoming various abiotic stresses either via modulating miRNAs using phytohormones or by controlling phytohormonal level using miRNAs as intermediate. The phytohormonal homeostasis and miRNA regulation walk parallel during abiotic stress responses, suggesting an interconnected network operating in regulating the genes responsible for abiotic stress tolerance Noman and Aqeel (2017). This functional regulation of phytohormones by miRNAs in response to various abiotic stresses encountered by plants. A salt tolerance protein (TC114805) was identified as the target of miR2708. Notably, miR2687 targets a gene coding xyloglucan endotransglucosylase/ hydrolase (XTH), which is recognized as a cell wall-modifying enzyme, participates in cell wall development and confers plant tolerance to abiotic stresses. These results indicate that Hg is able to alter significantly genes expression in Hg-treated plants and the Hg-induced gene regulatory frameworks will contribute a great deal to our understanding of the molecular mechanism for plant tolerance to Hg stress.

13. Summary and Conclusion

Mercury (Hg) is recognized as a toxic, persistent, and mobile contaminant; it does not degrade in the environment and becomes mobile because of the volatility of the element and several of its compounds. Moreover, mercury has the ability to be transported within air masses over very long distances. The global risk posed to humans and the wider environment by mercury (Hg) contaminated soils is severe. Mercury (Hg) contaminated soils constitute complex systems where many interdependent factors, including amount and composition of soil organic matter and clays, oxidized minerals (e.g. Fe oxides), reduced elements (e.g. S^{-2}), as well as soil pH and redox conditions affect mercury forms and transformation. Mercury can readily bind to colloids due to their high specific surface area and the presence of surface functional groups. Nano-sized mercury (Hg) particles as well as soluble mercury (Hg) complexes play an important role in mercury (Hg) mobility, availability, and methylation in soils

Over the last few decades, considerable scientific knowledge has been developed on the sources and emissions of mercury, its pathways and cycling through the environment, human exposure, and impacts on the environment and human health. Mercury (Hg) is the only element in the periodic table to have its own environmental convention, i.e., the Minamata Convention on Mercury, thus highlighting the importance of the Hg pollution issue. An improved understanding of the global mercury (Hg) cycle is important for our capacity to predict how regulatory efforts to reduce current emissions to air, water and land will affect mercury (Hg) concentrations in environmental compartments, biota and humans. Hg is released into the environment through human activities and via natural sources and processes, such as volcanoes and rock weathering. Following its release, mercury (Hg) is transported and recycled between the major environmental compartments.

Mercury (Hg) is considered a peculiar chemical element because it displays particularly, strong chemical and biological activity as well as variability in form (liquid and gaseous). Mercury (Hg) compounds with very different chemical and physical properties are included in various cycles of its natural circulation. Mercury (Hg) is a globally distributed pollutant due to characteristics such as low melting and boiling points, conversions between chemical forms and participation in biological cycles. In respect of anthropogenic emissions, the global atmospheric mercury (Hg) deposition rate is approximately three times higher than that in preindustrial times and has increased by a factor of 2–10 in and around the most industrialized regions. Mercury (Hg)-contaminated land environments pose a risk to global public health, with Hg being listed as one of the 'ten leading chemicals of concern'. In 2013, the United Nations (UN) introduced the 'Minamata Convention on Mercury', which aims for a more global effort for managing the risk presented by Mercury (Hg) to human health and the environment. Gene manipulation and molecular breeding of plant cultivars to minimize mercury (Hg) accumulation seems to be a prospective substitute to reduce the risk of Hg entering the human food chain.

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