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Impacts of Metal, Metalloid and Their Effects in Plant Physiology: A Review

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ABSTRACT

Due to anthropogenic activities effects of metal and metalloid toxicity are gradually increasing, furthermore contamination soil ranks among the most important factors, affecting crop yield production. The metals and / or metalloids can enter the food chain and, affecting on human health and alterations to the environment. Metalloids represent a wide range of elements with intermediate physiochemical properties between metals and non-metals. Metalloids, such as boron, selenium, and silicon are known to be essential or quasi-essential for plant growth. In contrast, metalloids like arsenic and germanium are toxic to plant growth. Metalloids toxicity is largely depending on their concentration within the living cells. Some of them are beneficial for plant growth and development particularly, at low concentration; however, high concentration has negative effects. Uptake mechanisms of metalloids by roots systems and their subsequent transport to different tissues and inter/intra-cellular redistribution have great importance. However, uptake of metalloids by plants has been well-studied .In addition various transporters, as well as membrane channels involved in these processes, have been identified. In order to overcome the biotic and abiotic stresses particularly, during mechanisms have been developed by plants. Metals and metalloids such as Zn, Cu, Al, Pb, Cd, and as, exert several effects on plants, the main strategies involve hyperaccumulation, tolerance, exclusion, and chelation with organic molecules. Recently omics era has increased knowledge on the plant genome and transcriptome plasticity to defend against these stimuli. Summarizing the relevant findings on the uptake mechanisms by plants, accumulate, transport, tolerate, and respond to this metal/metalloid stress. Furthermore, potential applications of biotechnology for improving plant tolerance or increasing the accumulation was also discussed.

Keywords: abiotic stress, plant tolerance, metal (oid) toxicity

1. Introduction

Metals and metalloid ions are a natural part of our planet and are present in the diverse layers that compose it. Metalloids are natural elements that possess shared properties between metals and non-metals and are present in the earth's crust. Commonly, metalloids occur in the environment together with a mixture of inorganic and organic compounds and other natural chemicals Kroukamp *et al., (*2016). Because of the indiscriminate industrial exploitation of these elements, metalloids can be found at particularly, high concentrations in some soils, with consequent deterioration of ecosystems and deleterious effects on plant growth and potential hazards to humans because of entry into the food chain Anjum *et al.,* (2014); Maksymiec, (2007); Prasad, (2004); Singh *et al., (*2011). The uptake of metalloids is an important physiological process and has a significant impact on plant development. The uptake and subsequent transport in plants are known to be driven by both active and passive processes

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Kroukamp *et al.,* (2016); Palaniappan and Karthikeyan, (2009); Rejomon *et al.,* (2010); Valvanidis and Vlachogianni, (2010). According to Eiche *et al*., (2015), metalloids' occurrence in plants is a natural effect, even though several agents such as microbial activities or weathering and geological events may increase their presence in soils and consequently, in plants. The involvement of metalloids in several chemical and biological processes is well known, thanks to speciation studies that offer information about the bioavailability, as well as the fate of metalloids Gräfe *et al., (*2014); Kroukamp *et al.,* (2016); Michalke, (2003); Ressler, *et al., (*2000); Stanislawska *et al., (*2013); Thomas, (2008); Vacchina *et al.,* (2003). These studies have shown various aspects that affect the mobility of metalloids, such as sorbent nature, pH, existence and quantity of organic and inorganic acids, root exudates and nutrients. However, when their levels are found in high concentrations, toxicity for many of they life forms (microorganisms, plants, animals, and humans) can result Kopittke *et al., (*2017), Rahman, and Singh (2019). In addition, human activity has largely contributed to their liberation from these natural sources, causing contamination of soils, rivers, oceans, and the atmosphere Narendrula-Kotha *et al., (*2019).This has, in turn, impacted the food chains (bioaccumulation) and posing severe risks to human health through the pollution of arable lands and diverse ecosystems Narendrula-Kotha *et al., (*2019), Gong *et al., (*2020). From an anthropocentric standpoint, the fact that many of these elements are now present in increasing concentrations represent a risk to global food security, along with various other forms of abiotic stress Gong *et al., (*2020). Recently, the distribution of this form of pollution in Europe, Africa, and China was revised Chmielowska *et al., (*2021). In Latin American countries, the main sources for this form of environmental contamination are extensive agriculture, industrial, and mining activities Di Marzio *et al., (*2019). Mining is considered as one of the main sources of metal (oid) pollution, since many of the world's metals and metalloids are extracted in Latin American countries Di Marzio *et al., (*2019). In fact, in Mexico, mining has been a very profitable commodity since colonial times; the country is still the top producer of silver along with other metals of economic importance such as gold, copper, and lead, among others Mendoza-Hernández *et al., (*2019). Important research has been done to analyze endemic, native, and invasive plants that can adapt to the conditions found in mine tailings, for example, the high concentration of copper found in ancient mining sites in Nacozari, Sonora, Mexico Santos, *et al.,* (2017).

Heavy metals and metalloids an important roles in plant development by participating in metabolic reactions and by acting as micronutrients (e.g., Fe, Co, Cu, Mn, Zn, and Mo) Rahman and Singh, (2019). Nevertheless, when they exceed their threshold concentrations, their actions are considered toxic to plant development. The main characteristic used to classify heavy metals is density, which has been revised elsewhere Rahman and Singh, (2019), Fryzova *et al., (*2017). In recent years, this term has been associated with the onset of a wide array of detrimental effects in plants. This is particularly, true for elements such as arsenic (As), cadmium (Cd), lead (Pb), and chromium (Cr), among others Rahman and Singh, (2019). Some other metallic elements, such as aluminum (Al), antimony (Sb), mercury (Hg), and nickel (Ni), among others, have also been studied to investigate their harmful effects in plant development when present above their threshold concentrations. For instance, aluminum toxicity in plants is related to the global increase in acidic soils (40% of the world's arable land), since its most toxic forms (Al^{3+}) are available under acidic pH values Fryzova *et al., (*2017). As stated previously, all metallic elements, whether they are related to plant development or not, have a threshold concentration beyond which deleterious effects and growth impairment are generated in plants Gong *et al.,* (2020). In addition, the soil pH value is a very important aspect, since some elements are more bioavailable at pH ≤ 7 Von Uexküll *et al., (*1995). The harmful effect of an element in plants and other life forms relies on the capacity of such metallic ions to compete with normally occurring ions that are important cofactors or ligands for vital enzymes in primary and secondary metabolism Rahman, and Singh, (2019). Their interactions with sulfhydryl groups generates an imbalance in protein functions and an increase in the plant´s oxidative state Clemens and Ma, (2016). In fact, they can displace important elements (e.g., Ca^{2+} and Mg^{2+}) present in cell walls and membranes; for example, Al, Cu, Pb, and Zn bind more readily to the cell wall pectins than Ca Fryzova *et al., (*2017). Evolution has played a fundamental part in the adaptation processes of land plants, by enhancing the attributes necessary to thrive under various environments. This has occurred through multiple events, including speciation, duplication, and gene fixation among their genomes Qiao *et al., (*2019). Hence, a plethora of complex mechanisms has developed in plant genomes to overcome abiotic stress. Plants also have the natural capability to thrive in metal- and metalloid-contaminated soils, which are a growing trend in many cultivable and arable lands worldwide Clemens and Ma, (2016). Several research groups have gained interest in unveiling the mechanisms involved in the interactions among plants and metals, with the purpose of understanding plant evolution and to take advantage of adaptation skills to utilize plants in phytoremediation strategies to alleviate the effects of increasing metal and metalloid concentrations in agronomically important soils around the globe Alloway, (2013). In this sense, the plant–metal(oid) interaction at high concentration levels increases the oxidative state of plants, generating more reactive oxygen species (ROS) Fryzova *et al., (*2017), sand depending on the nature of these plants, the use of pre-existing coping mechanisms will be triggered or the expression of certain machinery to deal with the danger will be induced. Most of this damage is generated in the first contact zone for potential hazardous metal (oids): the root. The root apical meristem (RAM), root cap, and root tip are the main sites for the first plant–metal (oid) interaction Yadav *et al., (*2021). This, in turn, generates severe anatomical and physiological alterations to the root system, such as growth inhibition by compromising the functionality of meristematic cells present in the RAM, and the internalization of metal (oid) ions can compromise elongation and proper root architecture formation Fryzova *et al., (*2017), Clemens, and Ma, (2016), Yadav *et al.,* (2021). Similar effects have been reported in lateral root primordia, where the presence of metallic ions generates cellular impairment and alterations in cellular hierarchy establishment in meristematic zones, leading to alterations in quiescent center (QC) formation Yadav, *et al., (*2021). Alongside this, root cortex tissues are compromised under conditions of metal and metalloid stress in plants, generating alterations in endodermal cells, deposition of suberin and lignin, cell wall thickening (exo and endodermal cells), formation of air spaces and alterations in intercellular spaces Clemens and Ma, (2016), Yadav *et al.,* (2021), and finally, modifications to the root vasculature (central cylinder, parenchymatic cells in the pith), along with dark deposit formation (e.g., As (III) in *Glycine max L.*) Yadav *et al.,* (2021), Armendariz *et al.,* (2016). Variations in the cell structure are not limited to the root system but protrude up to the stem tissues, disrupting cell division and enlargement in cortical cells and causing a loss of turgor in sclerenchyma cells in the vicinity of phloem cells, among other negative effects (e.g., after exposure to Cu, As, or Pb) Yadav *et al., (*2021). Foliar tissues are the final frontier for metal (oid) uptake via the roots; thus, part of a plant´s plan is to avoid the entrance of such metallic elements into photosynthetic tissues by limiting their entrance or translocation to them Clemens and Ma, (2016). However, completely avoiding this seems impossible in some plant systems, and therefore, negative effects appear, such as a reduction in leaf thickness, alterations to the epidermal cell structure and a reduction in intercellular spaces (mesophyll), an increase in callose deposition, and alterations to the stomatal structure, density, and aperture frequency (e.g., after exposure to Cd, As, and Mn) Yadav *et al.,* (2021), Pereira *et al., (*2017). Kim *et al.,* (2020), relevant information concerning metal and metalloid toxicity and the mechanisms exerted by either plants to tolerate or hyperaccumulate these elements in their cells. Particular interest is placed on plant evolution regarding accumulation and tolerance traits, the different mechanisms of transport used, accumulation, transcriptome analysis, signaling pathways involved in the response to metals, changes in plant cells under heavy metal and metalloid stress conditions, and, finally, approaches to the biotechnological and ecological application of plants for possible phytoremediation purposes

1. Metal and Metalloid Uptake, Toxicity and Transport in Plant

Active and passive transport are two important pathways followed by the plant for the cellular uptake of metalloids from the soil and their subsequent transport to aerial tissues Kroukamp *et al.,* (2016); Zangi and Filella, (2012). Initially, it was believed that the metalloids enter the cell just by passive ways. Several pieces of evidence suggest the involvement of integral membrane proteins in the uptake and/or exclusion of metalloids from the cell. The concentration gradient can drive the transport through these membrane-spanning proteins, that is, the difference in the solute concentration where the route of diffusion is from high to low concentration or via energy-fueled pumps where transport occurs against the concentration gradient Zangi and Filella, (2012).

Carrier proteins can work with a concentration gradient (passive transport), but some carrier proteins can move solutes against the concentration gradient (from low concentration to high concentration), with energy input from ATP. As in other types of cellular activities, ATP supplies the energy for most active transport. One-way ATP powers active transport is by transferring a phosphate group directly to a carrier protein. This may cause the carrier protein to change its conformation, which moves the molecule or ion to the other side of the membrane. Active transport, adenosine triphosphate

(ATP) is used as the energy source that is directly consumed by primary active transporters or by other ion-pumping proteins transporting Na^+ or H^+ and creates an electrochemical potential difference on both sides of the cell membrane Zangi and Filella, (2012) Fig. (1). This difference in electrochemical potential provides the force for transportand this type is referred to as secondary active transport, which is usually involved in the transport of ions Zangi and Filella, (2012).

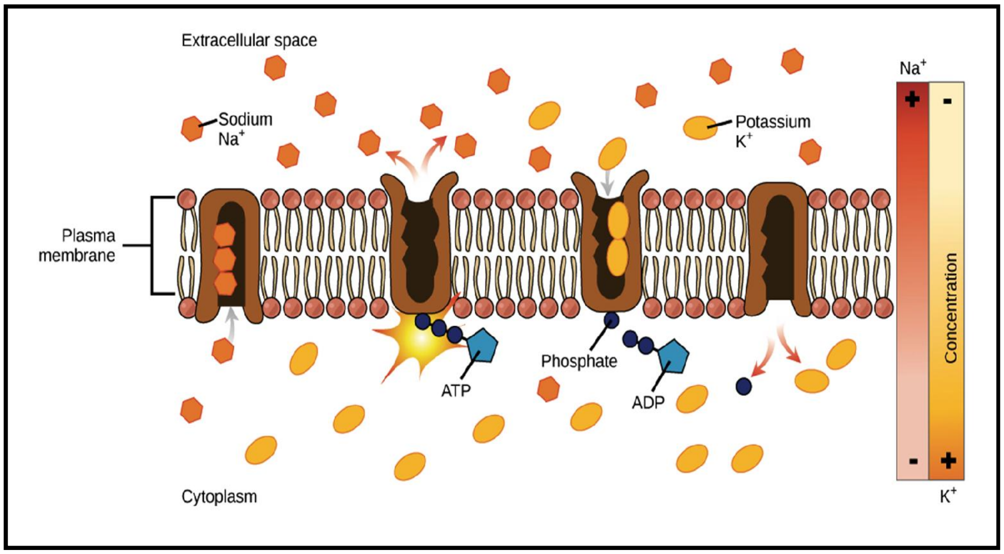

Fig. 1: Illustrates One-way ATP powers active transport is by transferring a phosphate group directly to a carrier protein. This may cause the carrier protein to change its conformation, which moves the molecule or ion to the other side of the membrane. An example of this type of active transport system

Metal and metalloid toxicity is generated by elements such as Cu, Fe, Mn, Zn, Ni, Co, and Al (some are considered micronutrients) and others, such as Cd, As, and Pb, that do not have biological relevance to plants and are associated with negative effects. Essential heavy metals are needed in minute quantities for vital functions (biochemical and physiological) Pauwels *et al., (*2005), Yadav (2010). When present above their threshold limits, all of these elements have different levels of toxicity in plants, which depend mainly on their concentrations and bioavailability in different soil types and have severe effects on the normal functioning of metabolic pathways by interfering or replacing pigments or enzymes and altering their original method of action Rascio and Navari-Izzo (2011), Palansooriya *et al., (*2020). The uptake and accumulation of heavy metals by plant roots occurs through an inter-related network of physiological and molecular mechanisms, including the binding of metals to extracellular exudates and cell wall components; compartmentalization of toxic metals from cytoplasm to the vacuoles; the formation of complexes of metals and amino acids, organic acids (OAs), MTs, or phytochelatin (PC); the production of heavy metal-induced antioxidative enzymes; and plant metabolism modification and repair and recovery of damaged cellular structures. Fig. (2).

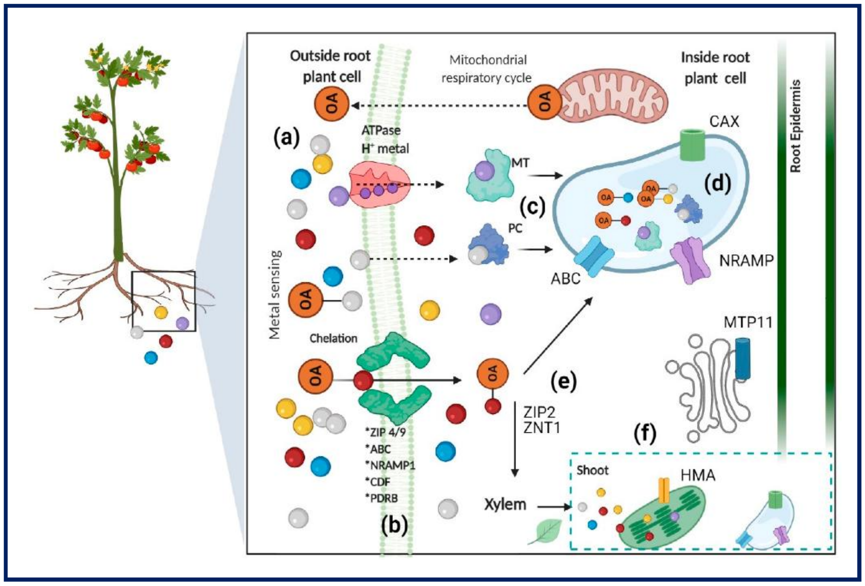

Fig. 2: Schematic representation of the physiological and molecular processes of absorption/translocation of metals into plants. The uptake of heavy metals ((e.g., Pb, Cd, As, Zn, etc.) (Colored circles)) Occurs through the root cells, where the presence or high concentration of these metals triggers different signaling pathways inside the cell. The metal sensing signals initiate a defense response in plants such as the release of mitochondrial-derived OAs that form complexes with the metallic ions outside the root cell (a), or the introduction of metals and metal–OA complexes to cells through transporters (ABC-type, ZIPs, CDF, ATPase H+ metal, etc.) (**b**). in the cytosol, these metals form complexes with protein chelators (MTs and PCs) (**c**) that are then transported into vacuoles, also by metal transporters (ABC-type, NRAMP, CAX, and MTP), to accumulate there or to another organelle such as the Golgi (**d**). Heavy metals also can be translocated to the xylem by transporters (ZIP2 and ZNT1) and ultimately transported to the shoots (**e**), where they can also be introduced into the cell vacuoles, Golgi (MTP11), and chloroplasts (HMA) by transporters (**f**). Orange circles represent organic acids (OAs). MT, metallothionein, PC, phytochelatin. After: Angulo-Bejerano, (2021)

These processes lead to changes to important physiological and biochemical processes, including adjustments to gene expression, protein variations, and alterations in the metabolite composition, all of which are responsible for the development of appropriate signals to activate defense and tolerance machinery in plants under conditions of heavy metal toxicity and detoxification mechanisms that may differ among plants and exposure to different metals or metalloids Fu *et al., (*2014), Berni *et al., (*2019), Fig. (3).

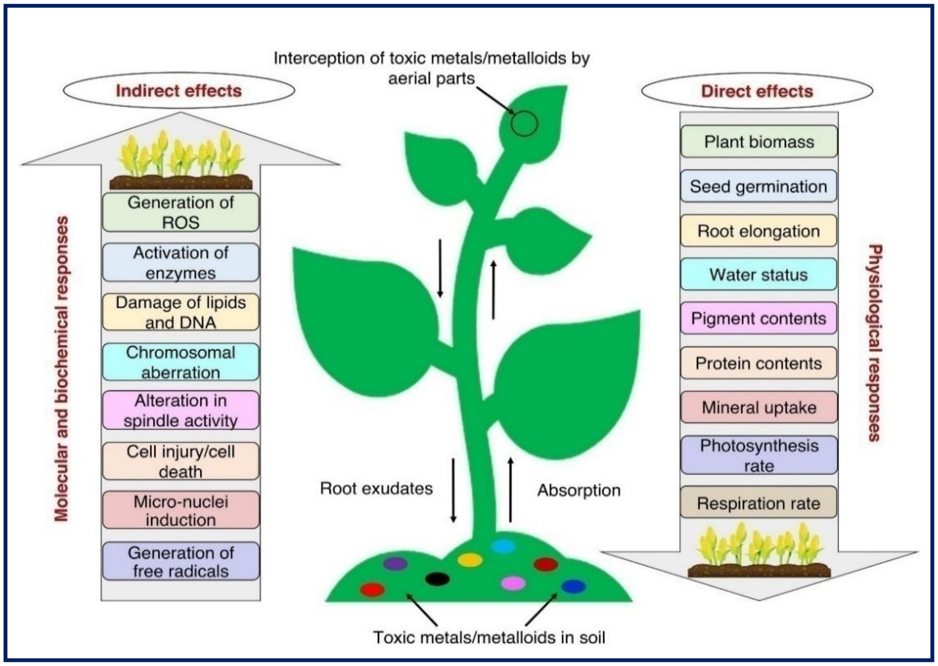

Fig. 3: Illustrates plant responses to toxic metals/metalloids toxicity with possible direct and indirect effects on crop productivity. Plants interact with toxic metals/metalloids via above ground and/or below ground parts. The toxic effects of several toxic metals/metalloids decrease the physiological responses and increase the molecular and biochemical responses. After: Raza *et al.,* (2022)

Raza *et al.,* (2022), reported that food safety has emerged as a high-urgency matter for sustainable agricultural production. Toxic metal contamination of soil and water significantly affects agricultural productivity, which is further aggravated by extreme anthropogenic activities and modern agricultural practices, leaving food safety and human health at risk. In addition to reducing crop production, increased metals/metalloids toxicity also disturbs plants demand and supply equilibrium. Counterbalancing toxic metals/metalloids toxicity demands a better understanding of the complex mechanisms at physiological, biochemical, molecular, cellular, and plant level that may result in increased crop productivity. Consequently, plants have established different internal defense mechanisms to cope with the adverse effects of toxic metals/metalloids. Nevertheless, these internal defense mechanisms are not adequate to overwhelm the metals/metalloids toxicity. Plants produce several secondary messengers to trigger cell signaling, activating the numerous transcriptional responses correlated with plantdefense. Therefore, the recent advances in omics approaches such as genomics, transcriptomics, proteomics, metabolomics, ionomics, miRNAomics, and phenomics have enabled the characterization of molecular regulators associated with toxic metal tolerance, which can be deployed for developing toxic metal tolerant plants. This review highlights various response strategies adopted by plants to toleratetoxic metals/metalloids toxicity, including physiological, biochemical, molecular stress-inducible phenotypes, and metabolic pathways that could potentially help plants to cope up with metals/metalloids toxicity in the face of fluctuating environmental conditions. Finally, some bottlenecks and future directions have also been highlighted, which could enable sustainable agricultural production. The symptoms of high metal concentrations in plants include chlorosis in young leaves moreover, growth inhibition due to a decoupling of photosynthetic enzymes Yang *et al.* (2020).Fig. (4).

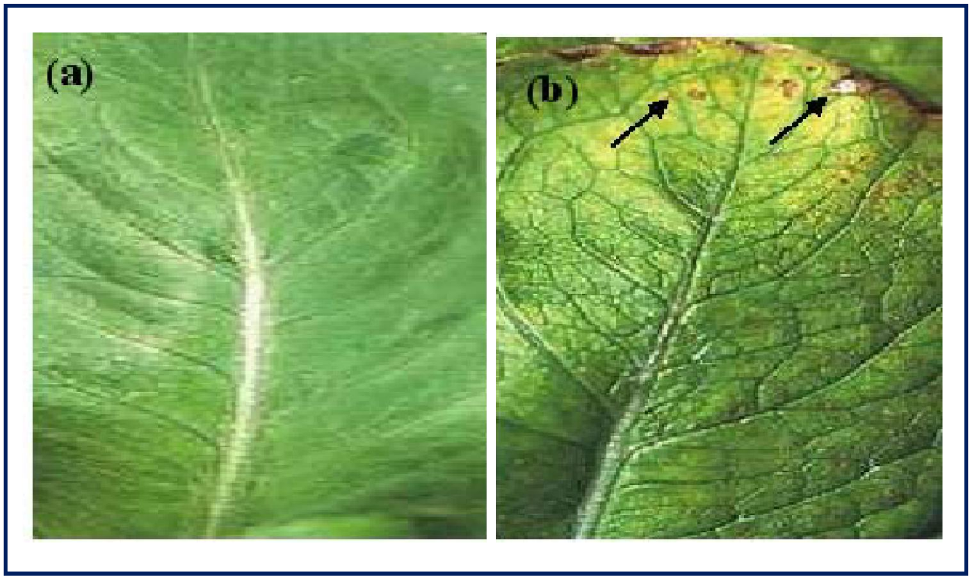

Fig. 4: Illustrates small chlorotic stippling on the old leaves of the plant. (a) Control plants, (b) plants collected from urban and industrial areas. Arrows indicate Chlorotic and necrotic lesions on leaves

Every battle in this fight for survival has a starting point; in the case of metal toxicity, the interaction between increasing soil metal concentration and root epidermis sensing and signaling seems to be the first step Jalmi *et al., (*2018). Once the plant has established a first defense line involving the exclusion and chelation of metal ions with OA, another strategy follows. In many cases, as previously mentioned, this relies on a metal concentration threshold Mehes-Smith *et al., (*2013). This strategy involves the tolerance or entrance of the complex formed by metallic ions and OAs into the cell (metal–OA complex). As described, the expression of transporters to liberate OAs and chelating compounds to neutralize these elements in the rhizosphere is one of the main strategies triggered in plants under conditions of metal/metalloid stress Fig. (5).

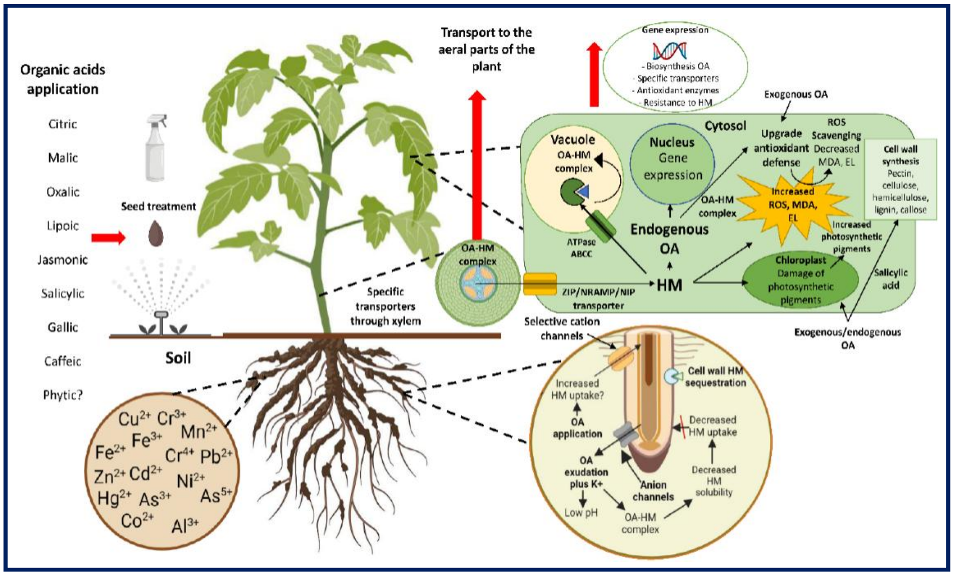

Fig. 5: Potential molecular and physiological mechanisms triggered by the exogenous application of organic acids that increase the tolerance of plants. After: Vega *et al., (*2022)

Transporters include zinc–iron permease (ZIP), heavy metal transport ATPase (CPx- and P1B-ATPase), natural resistant associated macrophage protein (NRAMP), cation diffusion facilitator (CDF), and ATP-binding cassette (ABC) transporters, which are present at the plasma membrane and on the tonoplast membrane of cells. These are used to introduce the chelated metals/metalloids into the plant cells and to translocate them into accumulating organelles (cell wall and vacuoles) in plant tissues (leaves) Singh *et al.,* (2016), Rizvi *et al., (*2020). ABC transporters are powerful transporters that drive the exchange of compounds across many different biological membranes, in most cases against electrochemical gradients using energy released from ATP hydrolysis Wilkens, (2015). They have been widely described as crucial elements in metal and metalloid toxicity in plants, which function as ATP-driven pumps, and their structure consists of two transmembranal domains (TMB), which are hydrophobic and form the membrane-spanning pores and two cytosolic domains. The latter domains are called "nucleotide binding domains (NBD)" or "nucleotide binding folds (NBF)" Kang *et al., (*2011).

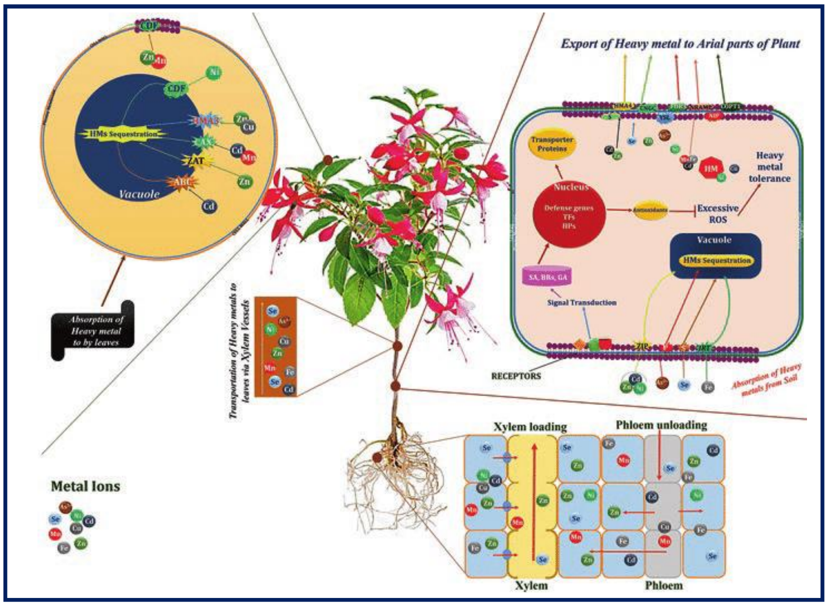

Fig. 6: Illustrates heavy metal uptake and transport in plants through various metal transporters on plasma membrane. After: Khalid, *et al., (*2019)

Khalid *et al., (*2019) reported that many factors regulate the uptake of metal ions from the soil, for example, the metal availability, soil aeration, soil moisture, pH, and temperature. Hence, heavy metal accumulation is not simple increase in concentrations inside the plant against increasing concentrations in the environment. Similarly, microorganisms and root exudates also influence the HMs availability and mobility patterns in the soil Wenzel, *et al.,* (2003). Some metals like Cd are more mobile in the soil as compared to the others; hence, they are taken up swiftly Spence, *et al., (*2014). Root proliferation system also influences the uptake of heavy metals Whiting, *et al.,* (2000). Whiting *et al., (*2000). Nevertheless, the rate of metal uptake by plants can be estimated by using biological accumulation factor (BAF) under a known set of environmental conditions:

$$\frac{\text{The concentration of heavy metal in the plant}}{\text{The concentration of heavy metal in the soil}}$$

To avoid metal ions uptake, plants secrete various organic substances through the roots into the soil. These root secretions act as first line of defense and prevent metal uptake into the cell by chelating the metal ions Marschner, (1995). For nutrients and metal ions uptake from the soil, plants possess highly specialized transport systems Fig. (6).These transport systems involve different mechanisms to carry metal ions. Most of the HMs move via highly evolved co-transporters and metal pumps on the cell membrane of root cells Pilon *et al., (*2009). These transporters are the membrane proteins present at the organ, tissue or at the whole plant level. The intracellular metal ions transport is controlled by a set of these proteins located across the cell membrane, tonoplast, and other subcellular membrane bounded organelles Krämer *et al., (*2007); Maestri *et al., (*2010). On the other hand, some of the HMs like Cd and Pb are very toxic even in traces. In addition, these heavy metals do not take part in any of the specialized biological functions in plants. For this reason, it is assumed that these do not have any specific transporters present on cell membrane for their movement. For cellular entry, these toxic metal ions move through wide range of transporters. The most common transporters involved in HM transport belong to ZIP family, NRAMP, CDF, and P1B-ATPases Guerinot, (2000); Williams *et al., (*2000); Takahashi *et al., (*2012). Overexpressing genes for these transporters have been noticed in hyper accumulator plants. Notably, their expression does not have any harmful impact on physiological homeostasis in plants, but instead they confer enhanced heavy metal tolerance Curie, *et al., (*2000); Verret *et al., (*2004). In hyper accumulator plants, expression of zinc–iron permease (ZIP) genes coding for cell membrane cation transporters have been observed irrespective of high Zn availability in the soil Weber *et al., (*2004). Contrarily, in non-hyper accumulator plants, their expression is highly dependent on soil Zn availability. Only detectable fraction of these transporters can be seen under Zn deficiency Assunção *et al., (*2010). In Zn hyper accumulator plant, Thlaspi caerulescens, genes coding for Zn transporters express all the times irrespective the Zn status of soil. Therefore, this elucidates the great ability of T. caerulescens's to accumulate high amount of Zn Pence *et al., (*2000). ZIP expression in plants is directly associated with capacity to accumulate metal ions and they play vital role in enhanced metal accumulation capacity of hyper accumulator plants Krämer *et al., (*2007). In roots of N. caerulescens, constitutive, high expression of NcZNT1 indicates its involvement in root-to-shoot long distance transport by maintaining Zn and Cd influx for xylem loading Lin *et al., (*2016). Overexpression of IRT1 in the root cells of Arabidopsis thaliana against iron (Fe) deficiency in the soil proves the role of IRT1 in the uptake of Fe from the soil Vert *et al., (*2002). Several other heavy metal transporters are present on the cell membrane, for example, in hyper accumulator plant Anemone halleri, AtHMA4 is involved in hyper accumulation and root-to-shoot translocation of Cd and Zn Hanikenne *et al., (*2008). In *Noccae acaerulescens ecotypes,* the difference in the expression of NcHMA3 and NcHMA4 is involved in rendering Cd tolerance Ueno *et al., (*2011); Craciun *et al., (*2012). NRAMP is another class of cell membrane-bound metal transporters involved in the transport of different metal ions (e.g., Ni, Cd, Zn, Mn, and Co). These transporters are localized on the tonoplast and the cell membrane of root and shoot cells Nevo and Nelson, (2006). OsNRAMP1 is known to transport Fe through endodermis and pericycle cell membranes in rice. Expression of OsNRAMP1 greatly increased the Cd and As tolerance in roots and shoots of Arabidopsis thaliana Tiwari *et al., (*2014). Arsenic (As) enters the cell through phosphate transporters since it is proved analogous to phosphate in chemical structure Meharg and Hartley-Whitaker, (2002); Kanoun-Boulé *et al., (*2009). Different phosphate/arsenate transporters are present on hyper accumulator plant Pteris vittata as compared to Pteris tremula, a non-hyper accumulator Caille *et al., (*2005). Similarly, Galeas *et al., (*2007) attributed much higher concentrations of Selenium (Se) and Sulfur (S) in Se hyper accumulator plants Stanley apinnata and Astragalus bisulcatus as compared to nonhyper accumulators. This helps us to build opinion that the sulfate transporters in the cell membrane of roots are involved in Se uptake due to structural similarity between the two elements.

These types of transporters are well represented in different organisms and are highly conserved among species. Compounds that originate in the cytoplasm are pumped out of the cell by ABC transporters, and they allow the entrance of compounds generated outside the plant cell and into intracellular organelles (endoplasmic reticulum, mitochondria, vacuole, and peroxisome, among others). The organisms with more complex functions require a greater number of transporters to exchange metabolites and information between cells and organs. In plants, the ABC and secondary active transporters have great relevance in the development, nutrition, abiotic stress defense, and overall interaction with the environment Hwang *et al., (*2016). The AtABCC1 and AtABBC2 genes are important for metal access and sequestration into vacuoles, and their participation under conditions of metal stress has already been described for Cd (II), As, and Hg (II), among others. AtABCC1 participates in the transport of xenobiotics by folate glutathione S-conjugates, whereas, AtABCC2 and AtABCC3 carry out the transport of glutathione S-conjugates, mainly xenobiotics, among other compounds Frelet-Barrand *et al.* (2008). Further, some plants translocate the metal–OA complexes to the aerial parts of the plant by activating the expression of different metal transporters into the xylem to efficiently move these complexes to their final storage destination. We cover some examples of the effects, both physiological and molecular, of metals and metalloids that are of biological relevance but are toxic in high concentrations (Zn and Cu), others that could have some beneficial effects in plants (Al), and finally, toxic elements (Pb, Cd, and As) with adverse impacts on plant functions. We emphasized the cellular response to counter the toxic effects and provide a molecular and biotechnological approach to the possible use of accumulative and hyper accumulative plants. Others. AtABCC1 participates in the transport of xenobiotics by folate glutathione S-conjugates, whereas AtABCC2 and AtABCC3 carry out the transport of glutathione S-conjugates, mainly xenobiotics, among other compounds Frelet-Barrand *et al.* (2008). Further, some plants translocate the metal–OA complexes to the aerial parts of the plant by activating the expression of different metal transporters into the xylem to efficiently move these complexes to their final storage destination.

3. Role Cell Membrane Proteins in HMS Tolerance in Plants

3.1. The Reorganization of Endomembrane

When plants are exposed to HMS, the plasma membrane, as the first biological barrier, plays an important role in protecting cells from the damage and toxicity caused by the metals Minami *et al.,* (2017). Plasma membranes are mainly composed of membrane proteins and lipids Cassim *et al.,* (2019). Here, we will discuss the role of proteins in membrane remodeling. A large number of studies have shown that the content of lipids, phospholipids, glucolipids, and sterols in the membrane are significantly changed under abiotic stresses such as HMS and high salinity Sarabia *et al.,* (2019), Rawat, *et al.,* (2021). This means that in response to abiotic stresses, plants reshape their membrane lipid composition and use this process to recruit many membrane proteins to resist HMS. For example, the metal ion efflux pump De Caroli, *et al.,* (2020), glutathione transferase Bellini *et al.,* (2020), aquaporin Barozzi *et al.,* (2019) and some other proteins have been related to toxic metal ion efflux, compartmentalization, and detoxification. Therefore, the reorganization of plant endomembrane under HMS is an important process to ensure lipid redistribution and metal homeostasis, because these membranes determine the location and functions of membrane proteins.

3.2. Detoxification Mechanism

Plants have evolved various mechanisms to detoxify excessive or small amounts of metal-like or heavy metal (HM) ions that include, but are not limited to the following: **(a)** reducing the absorption of HMs, **(b)** compartmentalization of metals, and **(c)** reducing the toxicity of metal ions (via chelation) Emamverdian *et al., (*2015), Sharma *et al., (*2016). These mechanisms are closely related to ion channel proteins and transporters in the membranes Vishwakarma *et al., (*2019). The members of these proteins are diverse and have different specificity for metal ions, while they differentially regulate the transport of metal ions in the horizontal or vertical directions in plant cells Fig. (7).

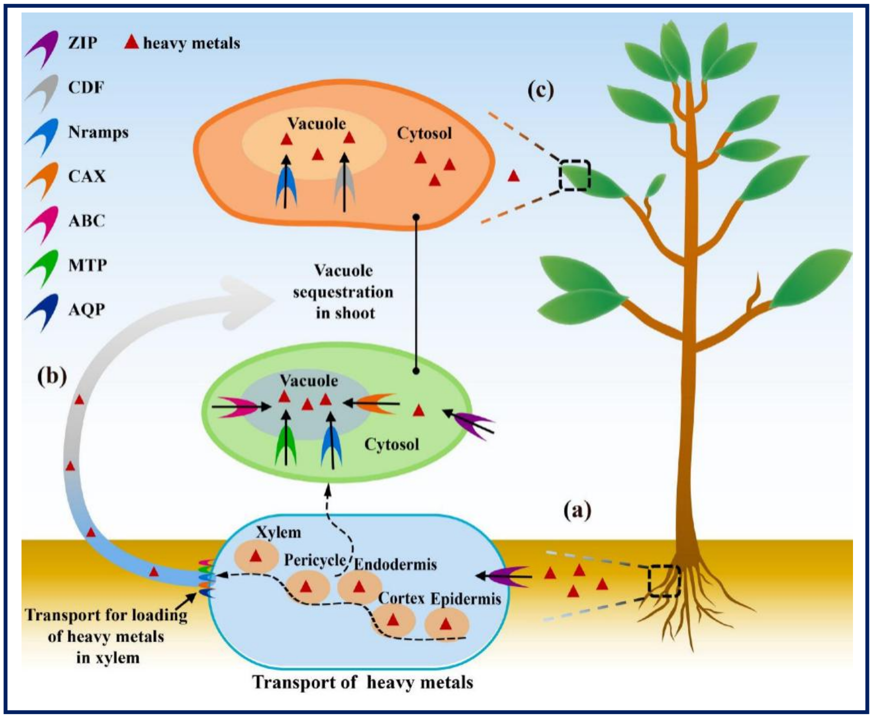

Fig. 7: Illustrates the role of transporters in plant responses to HMS. (a) Absorption of HMs in the roots by Zrt/Irt-like protein (ZIP). (b) Transport and loading of HMs from root to shoot, and their sequestration in vacuole as accomplished by various transporters such as ATP-binding cassette (ABC), cation/proton exchanger (CAX), natural resistance associated macrophage protein (NRAMP), metal tolerance protein (MTP), and aquaporin (AQP). (c) Vacuolar sequestration of HMs in leaves by cation/proton exchanger (CDF) transporters. The role of transporters in plant responses to HMS. (a) Absorption of HMs in the roots by Zrt/Irt-like protein (ZIP). (b) Transport and loading of HMs from root to shoot, and their sequestration in vacuole as accomplished by various transporters such as ATP-binding cassette (ABC), cation/proton exchanger (CAX), and natural resistance-associated macrophage protein (NRAMP). After: Wu *et al.,* (2021)

In plants, the main metal membrane protein families include Zrt/Irt-like proteins (ZIPs) Kimura *et al., (*2016), ATP - binding cassette (ABC) transporters Zhang *et al., (*2018). Cation diffusion facilitator (CDF) transporters Barber-Zucker *et al.,* (2020), metal tolerance proteins (MTPs) Zhang *et al.,* (2018), natural resistance-associated macrophage proteins (NRAMPs) Gao *et al., (*2020), cation/proton exchanger (CAXs) transporters Yokosho *et al.,* (2021), aquaporins (AQPs) Modareszadeh *et al.,* (2021) and many others. Zn and Fe mainly regulate the members of the ZIP family, and they participate in the transport of Zn, Fe, Mn, Cd, and Co in the roots of plants. OsZIP9 promotes the absorption of Zn and Co by rice roots Yang *et al.,* (2020). VsRIT1 is involved in Cd uptake in alfalfa roots Zhang *et al.,* (2020). The ABC transporters belong to the large-scale protein family and are widely distributed in a variety of organisms. ABC transporters can be divided into eight ABCA-ABCI subfamilies in terms of their phylogeny. The ABCH group is not reported in plants Kretzschmar *et al.,* (2011). Most of the members of the ABC family are located in the plasma membrane and tonoplast, while tonoplast-located ABCs play the role of metal detoxification by immobilizing metal ions in vacuoles Dahuja *et al.,* (2021). The CDF transporters play important roles in the homeostasis and tolerance of bivalent metal ions in plants. It can isolate metal ions in vacuoles and consequently reduce the toxicity of HMs in plants Song *et al.,* (2010). The NRAMPs are an evolutionarily conserved important metal transporter family and are responsible for the absorption and transport of divalent cations Ullah *et al.,* (2018). Studies have shown that vacuolar localization AtNRAMPs 3/4 are involved in the regulation of manganese homeostasis in Arabidopsis thaliana Lanquar *et al., (*2010), while AtNRAMP1 is known to reduce the toxicity of Mn and Zn in peanut plants Wang *et al., (*2019).

Membranes 2021, 11, x FOR PEER REVIEW 3 of 29 are diverse and have different specificity for metal ions, while they differentially regulate the transport of metal ions in the horizontal or vertical directions in plant cells Fig.(7), in plants, the main metal membrane protein families include Zrt/Irt-like proteins (ZIPs) Wang *et al., (*2019)**.**

4. Impact and Responses of Metal and Metalloids in Plants

4.1. Physiological Function of Zinc in Plants

Zinc (Zn) is one of the main metals required for all live forms; it participates in many enzymatic activities, Zn is part of some transcription factors, and is a cofactor for a great number of proteins Castillo-González *et al., (*2018). The toxicity of Zn depends on its bioavailability, concentration, and exposure time, the plant genotype, and plant development steps. The main symptom of Zn toxicity in plants is the growth inhibition of young, greened leaves in seedlings possibly due to reduced Fe^{2+} and Fe^{3+} intake, which may lead to cell death, growth changes caused by mitosis inhibition Reis *et al.,* (2018), and a reduction in biomass production as a result of photosynthetic machinery decoupling Fig.(8).

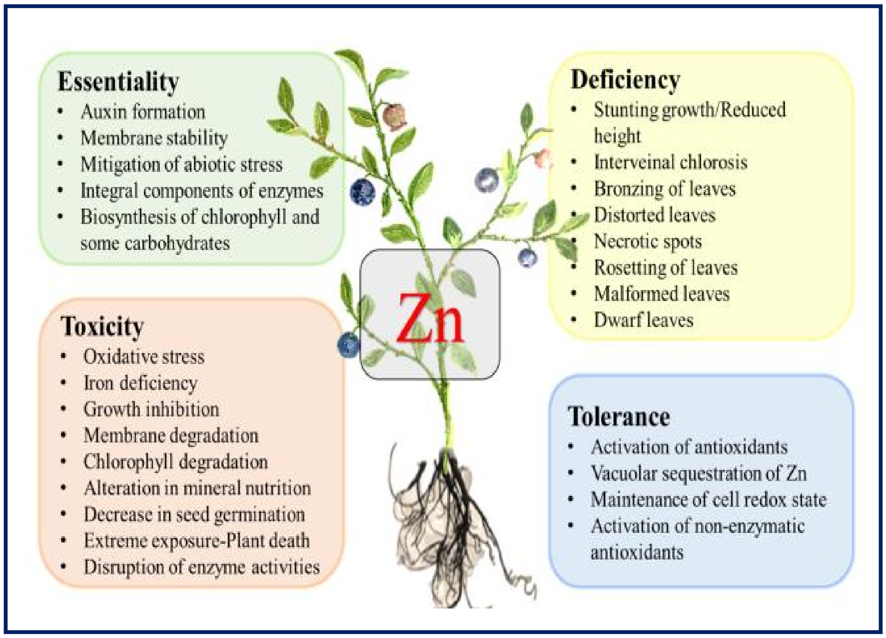

Fig. 8: Illustrates Zinc in Plant, Soil and Human system

This leads to a decrease in the total chlorophyll content and an increase in the levels of H_2O_2, malondialdehyde (MDA), and lipoxygenase activity Goodarzi *et al., (*2020). However, in the presence of high Zn concentrations, plants are prone to upregulation of the expression of Zn transporters and upregulation of a complex network of Zn detoxification mechanisms to overcome this stress Ricachenevsky *et al., (*2015). Nicotianamine serves as a chelator molecule for Zn, forming complexes with Zn (II), and interestingly, glutathione, PCs, and MTs can bind to Zn Pochodylo *et al., (*2017), Grennan, (2011). Some other types of chelators, such as citrate and malate, are both relevant in the Zn detoxification process. In fact, FRD3 (ferric reductase defective) participates in the root to shoot translocation of zinc and in citrate exudation Pineau *et al., (*2012). Furthermore, the zinc-regulated transporter (ZRT)/iron-regulated transporter (IRT) like proteins (ZIP) constitute a vast group of Zn transporters that are well characterized in plants. They participate in the primary uptake of Zn from the soil. Other important Zn transporters include AtMPT1 (metal tolerance protein 1), a tonoplast-associated protein that allegedly functions under conditions of basal Zn excess Delhaize *et al., (*2012) Fig. (9). Its role is to sequester Zn and introduce it into vacuoles of young, dividing cells in shoots, generating a storage point in these tissues. Additionally, the expression of AtMPT increases under conditions of Zn, Mn, and Cd excess and Fe deficiency Gustin and Zanis, (2011), Ricachenevsky *et al., (*2015). Excessive Zn levels are detoxified in part with the help of AtHMA3, and if this protein is absent, cytoplasmic levels of Zn cause an overload in chloroplasts Seigneurin-Berny *et al., (*2006). AtPCR2 is a gene that encodes the plant cadmium resistance (PCR) protein in A. thaliana and is related to Zn tolerance due to root–shoot translocation Song *et al., (*2010). Yellow stripe (YS) and yellow stripe-like (YSL) proteins have also been associated with Zn transport in both monocot and dicotyledonous plants, respectively. The first were formerly described in maize as Fe^{+3}phytosiderophores (transporting the metal from the rhizosphere to root cells), and they are capable of transporting Zn^{2+} phytosiderophores Schaaf *et al., (*2004). AtYSL1 and AtYSL3 are genes found in A. thaliana that participate in Zn remobilization from the leaves to the seeds during senescence. Phytotoxical effects of Zn can be reverted by the addition of several compounds in plants, including proteins, phytohormones, and chemicals.

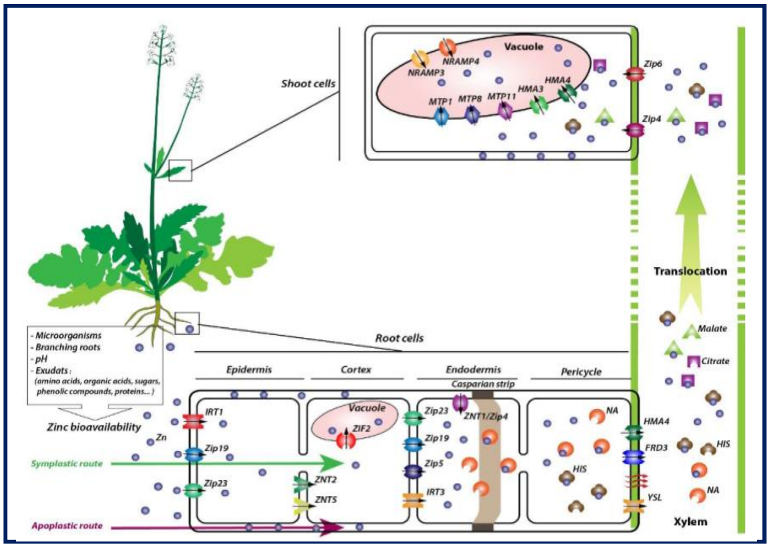

Fig. 9: Illustrates a model of the mechanisms that occur in hyperaccumulation plants upon exposure to zinc (Zn): Zn ion uptake, chelation, transport, and sequestration. Zn bioavailability can be influenced by several factors, such as microorganisms, branching roots, pH, and exudates. Once adsorbed by the roots, Zn can be absorbed by an apoplastic route: A passive diffusion through cells, or by a symplastic route via transporters. Within the latter path, Zn absorption by epidermis cells is mainly promoted by IRT1, ZIP19, and ZIP23. To reach the cortex, Zn can be directly diffused or by means of ZNT2 and ZNT5. Then, Zn can either be stocked in vacuoles (promoted by ZIF2) or transported to the endodermis through the following transporters: ZIP23, ZIP19, ZIP5, and IRT3. Zn following the apoplastic route is stopped by the Casparian strip, and then enters the endodermis via ZNT1/ZIP4. At this level, Zn can be chelated by nicotianamine (NA) or directly diffused to pericycle cells where a part can also be associated to histidine (His). The unchelated Zn can reach the xylem through direct diffusion or via YSL, ferric reductase defective 3 (FRD3,) and HMA4. Zn then crosses the xylem as a Zn-free form or coupled with His, citrate, or malate. To enter the leaf cells, Zn can passively penetrate in chelated forms or as the Zn-free form via ZIP4 and ZIP6 proteins. It is then sequestrated inside the vacuole through MTP1 (metal tolerance proteins 1). After Habiba Balafrej *et al., (*2020)

Habiba Balafrej *et al., (*2020), reported that zinc uptake particularly in the rhizosphere root zone is the first area of contact between metal and plants. In the soil, Zn occurs preferably in a crystalline form in iron-magnesium minerals, such as sulfide (ZnS). Zn is largely adsorbed in changeable forms, mainly as Zn^{2+}, $ZnOH^{+}$, and $ZnCl^{+}$, onto clay surfaces and organic matter Moreira *et al., (*2018). Roots generally absorb zinc as Zn^{2+} ions except at high pH, where it is absorbed as ZnOH Li, (2019). Many transporters belonging to the zinc-regulated transporter/iron-regulated transporter-like proteins (ZRT-IRT-like protein or ZIP family) and involved in Zn radial transport to the stele in roots have been identified. In N. caerulescens, NcZNT1, a major contributor to Zn transport across the endodermal cell, was isolated Van de Mortel *et al., (*2006) Constitutive overexpression of NcZNT1, a plasma membrane-located metaltransporter, in A. thaliana enhanced the tolerance to excess Zn exposure and increased the accumulation of Zn compared to wild-type plants Li, (2019). Furthermore, NcZNT 2 and 5, respectively orthologs of A. thaliana iron-regulated transporter 3 (IRT3) and ZIP5, are involved in Zn transport in the roots Van de Mortel *et al., (*2006), Fasani (2012). Additionally, IRT3 was detected in the plasma membrane of A. halleri cells in the roots after exposure to Zn Lin *et al., (*2016), Talke *et al., (*2006), Caldelas and Weiss, (2017). Interestingly, high levels of IRT3 expression were found in the roots of Zn-hyperaccumulating species, such as A. halleri and N. caerulescens Moreira, *et al., (*2018), Talke, *et al.,* (2006),. Other studiesconducted by Shanmugam *et al., (*2013) showed that IRT1 located in the plasma membrane is involved in Zn transport. Lin *et al.,* (2016), also observed a subcellular location of this transporter in the plasma membrane, which confirms its importance in the passage of these ions to the cellular cytoplasm. ZIP19 and ZIP23 expression was significantly induced in A. halleri and N. caerulescens roots in the presence of Zn Lin *et al., (*2016). In A. thaliana, high levels of ZIP19 and ZIP23 expression were observed in a Zn deficient culture medium Humayan *et al., (*2014), which suggests that the upregulation of these two genes in A. halleri and N. caerulescens might be correlated with a low Zn content in the rhizosphere due to the high activityof heavy metal ATPase 4 (HMA4) (involved in Zn translocation from the xylem to aboveground parts) Merlot *et al., (*2018), Lin, *et al., (*2016) Fig. (9).

The application of H_2S gas to the roots of Solanum nigrum L. reduces Zn-induced growth inhibition by enhancing the expression of several antioxidative enzyme genes and MT while decreasing Zn accumulation Liu *et al.,* (2016). The exogenous foliar application of 24-epibrassinolide (EBL) and 28-homobrassinolide (HBL) in Raphanus sativus L. was shown to enhance the levels of ascorbate (ASA), glutathione (GSH), and proline to confer resistance to radish plants against Zn^{2+} stress with positive effects on the restoration of photosynthetic pigments Ramakrishna, and Rao, (2015). Additionally, in Zn-stressed seedlings of Carthamus tinctorius L., oxidative damage can be reverted by the exogenous application of melatonin, GSH, or a combination of both with increments in ascorbate ASA, GSH, and PC Goodarzi *et al., (*2020).

4.2. Effect and response of Cu on ROS in plant

Plants require low quantities of toxic metal to act as parts of different metalloproteins and as cofactors for many different metabolic pathways involved in plant development and growth. In this sense, Cu is an essential element for the proper activity of plastocyanin, cytochrome oxidase, superoxide dismutase, and ascorbate oxidase as part of the antioxidant defense Viehweger, (2014). Accordingly, the Cu content in leaves is estimated to be 10 $\mu g. g^{-1}$ dry weight; higher concentrations are considered toxic in many plant systems Marschner, (2002). Within plants, copper is primarily transported in its reduced form. Many Cu transport proteins direct uptake, mainly the COPT/Ctr-like protein family Fig. (10). The expression of COPT/Ctr proteins depends on the availability of the Cu cation in the rhizosphere, growth stage, tissue involved, and local environmental conditions, which illustrate that Cu uptake is developmentally and environmentally regulated Yuan *et al.,* (2011). Among several proteins, COPT1 is the foremost required for Cu acquisition from soil. COPT1 is a high-affinity Cu (I) transporter located primarily at the root tip. Copper deficiency directs activation of COPT1 in an SPL7-dependent fashion, promoting effective Cu acquisition from the culture medium. Its acquisition within the cytosol stimulates the production of OH- in the cell, which interacts directly with non-selective cationic channels (NSCC). NSCC, being an ion channel, can stimulate the entry of Cu2 into the root and influence the ingress of other minerals as well Printz *et al.,* (2016), Yuan *et al., (*2011). Copper deficiency also activates COPT2 protein in an SPL7- dependent mode. COPT2 is present mainly in green tissues and is reported to occur in the differentiation zone of roots and in epidermal cells of root hairs and secondary roots.

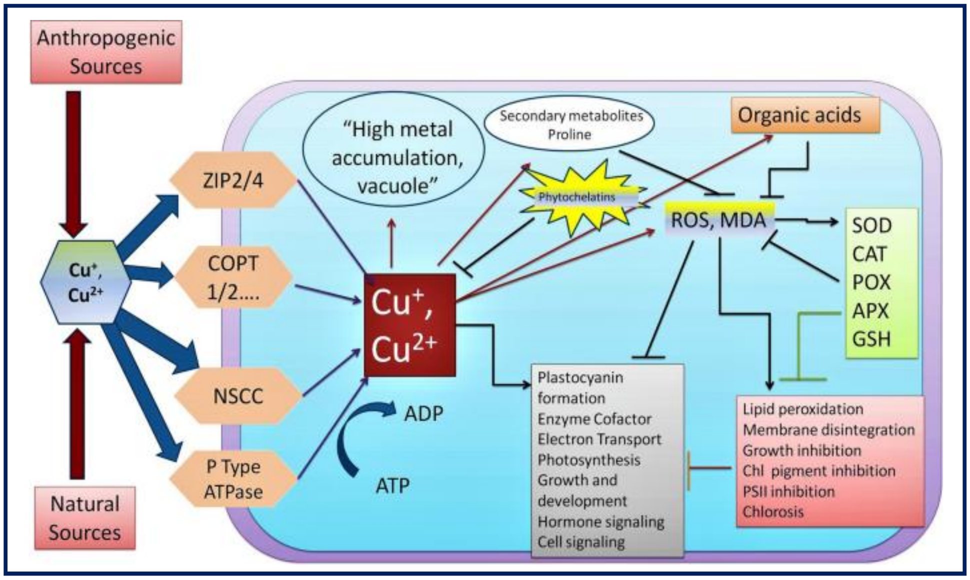

Fig. 10: Illustrates overview of copper uptake, and roles (essential and harmful) in plants. Copper is absorbed in plants by Cu trafficking proteins viz COPT/Cry family proteins (COPT1, COPT2, COPT3 etc.) as well as via Ptype ATPas and ZIP proteins. In adequate quantities, Cu is required for proper growth and development in plants and performs vital roles in plastocyanin biosynthesis and enzyme functioning, as well as regulation of important physiological and biochemical processes like photosynthesis, the electron transport system, hormone signalling and plant signalling. In excess concentrations, Cu inhibits plant growth and development by inducing various lipid peroxidases and reactive oxygen species. Excess accumulation enhances production of defense mechanisms including antioxidant enzymes, secondary metabolites and phytochelatins, which ultimately reduce toxicity to some extent. After: Anayat *et al., (*2021)

However, copper uptake from soil by COPT2 is restricted and functions as an alternate route for Cu absorption. Other Cu transporter proteins of the COPT/Cry family include COPT3, COPT4, COPT5, and COPT6. COPT3 and COPT5 act as secondary Cu transporters and are required in intracellular transport of Cu into cells. Both COPT 3 and COPT5 possess a single methionine- and a histidine-rich box, whereas COPT 4 lacks methionine residues. COPT 5 is localized on the tonoplast and is expressed in cotyledons, roots, leaves, and reproductive tissues. COPT6 has been recognized recently as a COPT/Cry family member and is responsible for Cu transport in seeds and leaves (Jung *et al.,*2012; Printz *et al.,*2016). PType ATPases Heavy metals like Cu1, Cu2, Zn2, Cd2, and Pb2, some of which are toxic, are transported through the plasma membrane via PType ATPase metal transporters Fig. (10)**.** These transporters require ATP to convey various cations across the plasma membrane and are classified into two types, i.e., 1 A ATPase and 1 B ATPase. Type 1 B ATPase is further subdivided into monovalent and divalent cation transporters Kumarm *et al., (*2020). Eight members of the type 1 B ATPase are identified in the genomes of rice (Oryza sativa) and Arabidopsis thaliana and are recognized as HMA transporters (AtHMA1–AtHMA8). Among them, Cu controls the translation of four HMA transporters, i.e., AtHMA5, AtHMA6, AtHMA7 and AtHMA8, which are strongly correlated to the type 1 B sub-family Kumar *et al., (*2020). AtHMA5 is regulated by higher Cu concentrations and eliminates excess Cu by symplast transport for xylem loading. In cucumber, two recognized homologs of AtHMA5 protein, i.e., CsHMA5.1 and CsHMA5.2, were reported to be allied with the vacuolar membrane, in contrast to the rice OsHMA5, which is localized in the plasma membrane Deng *et al., (*2013); Migocka *et al., (*2015). The differential expression of CsHMA5.2 with changes in Cu availability, particularly its elevated expression at high Cu levels, suggests the role of CsHMA5.2 for increased sequestration of Cu in cases of potential Cu toxicity Migocka *et al., (*2015). In contrast to CsHMA5.2, the plasma membrane-localized rice homolog OsHMA5 is suggested to be associated with metal efflux and not in metal sequestration into the vacuole, which highlights the species-dependent roles exerted by these HMA5 homologs. AtHMA7 regulates ethylene signaling by reacting with transcyclooctene (an ethylene receptor), expressing the characteristic feature of Cu in the ethylene-signaling pathway Li *et al., (*2017). AtHMA7 additionally delivers Cu to the secretory pathway, which is essential for the organization of ethylene receptors Hoppen *et al., (*2019). AtHMA6 and AtHMA8 mediate the transfer of Cu to plastocyanin, which is essential for sustaining photosynthesis during Cu deprivation in plants. AtHMA6 also delivers Cu to the chloroplast, where it is supplied as a cofactor in Cu/Zn SOD Zhang *et al.,* (2018a, b). In Oryza sativa, activation of ZIP1 in the endoplasmic reticulum was required to maintain proper allocation of Cu in cells; however, excess Cu led to upregulation in the ZIP1 transporter Liu *et al.,* (2019a); Kumar, (2020). Copper is an essential mineral element for plant growth and development Fig. (11). Copper plays a significant role in cell wall metabolism, photosynthesis, respiration, carbohydrate metabolism, chlorophyll biosynthesis, and oxidative phosphorylation.

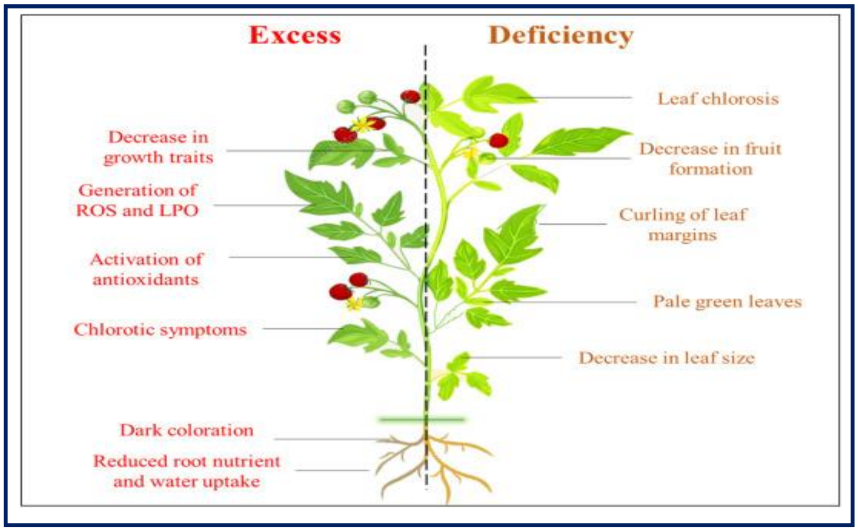

Fig. 11: Copper deficiency and toxicity symptoms in plants

Additionally, an optimal Cu concentration is a prerequisite for the activities of numerous enzymes, mostly for neutralizing oxidative stress response in plants Yruela, (2009). It also acts as a cofactor in various enzymes Marschner, (2011). For instance, Cu-associated proteins are active throughout the cell, as required in the electron transport chains of the chloroplast (plastocyanin) and mitochondria (cytochrome c oxidase). They are also essential for antioxidant enzymes in the cytosol and chloroplast (Cu/ZnSOD) Festa and Thiele, (2011), endomembrane (including the ethylene receptor) Rodrıguez *et al., (*1999a& b), and apoplast (laccase, polyphenol oxidases and other multicopper oxidases) Choi and Davidson, (2011). Other members of copper oxidases include amine oxidase enzymes allied to the cell wall which catalyze the oxidation of putrescine to generate H_2O_2 required in lignification, cross-linking of cell wall proteins and programmed cell death Møller and McPherson, (1998); ascorbate oxidases localized in the apoplast which regulate its redox state, and laccases also localized in the apoplast which play a role in lignification Hoegger *et al., (*2006); SKU5 (multi-copper oxidase-like proteins), important for synthesis of the cell wall Sedbrook *et al., (*2002); and polyphenol oxidase found in the thylakoids which is involved in ROS defense. In addition, Cu is required for synthesis of the ethylene receptor (ETR1) Rodrıguez *et al., (*1999a & b). Copper is a component of the photosynthetic electron transport chain, for CO2 assimilation and ATP synthesis Yruela, (2009). Copper is involved in photosynthetic reactions of PSII independent of plastocyanin Barr and Crane, (1976); Lightbody and Krogmann, (1967) Fig. (12).

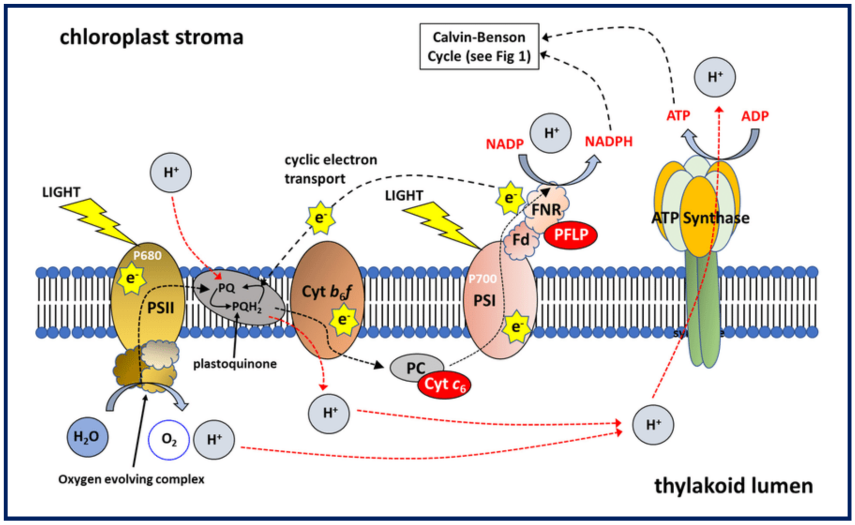

Fig. 12: Schematic Representation of Photosynthetic Electron Transport. Photosystem I (PSI), Photosystem II (PSII), Cytochrome b6f complex (Cyt b6f), plastocyanin (PC), Ferredoxin (Fd) and ferredoxin-NADP reductase (FNR). Cytochrome c6 (Cyt c6) transfers electrons from the Cyt b6f complex to PSI at a faster rate than observed for PC; plant ferredoxin-like protein (PFLP) After: Simkin *et al., (*2019).

Kumar *et al., (*2021), Singh *et al., (*2017) they reported that alterations triggered by Cu in plants, have some effect on several vital cellular processes such as photosynthesis, electron transport, cell wall metabolism and senescence, increases in proline, chlorophyll and H2O contents, and effects on P uptake in roots via transporters . Cu also elicits an imbalance in the overall redox state of cells by ROS production and lipid peroxidation. Furthermore, ROS generated by Cu are capable of reacting with thiol groups through Fenton chemistry, causing severe changes in protein structure, altering the proteins' functions, with subsequent effects on metabolic pathways, and causing damage to DNA and other biomolecules Hänsch and Mendel, (2009) , furthermore changing the antioxidant machinery of the cell Yadav *et al., (*2005).The oxidative stress caused by Cu also increases the H_2O_2 level, causes lipid membrane damage, leads to the accumulation of Cu in roots and shoots, and results in developmental inhibition (biomass reduction) and ion liberation from cells, which causes damage to proteins and nucleic acids Thounaojam *et al., (*2012). To avoid the generation of ROS, intracellular Cu is chelated and delivered to its partner proteins by specific chaperones such as CCH and ATX1 (for Antioxidant Protein 1), which mediate the transfer of Cu to Cu-transporting ATPases Shin *et al., (*2012). Sodium nitroprusside (SNP) is a NO donor that could also help to reduce the metal toxicity elicited by Cu, Cd, Al, and As in plants Panda *et al., (*2011), Zhang *et al., (*2008). However, plants also possess detoxifying mechanisms for cytotoxic compounds formed by reactions with Cu. Nitric oxide (NO) is involved in signaling pathways that, in many cases, lead to the activation of genes that participate in redox and defense activities, which help the plant to establish defense responses to overcome stress Siddiqui *et al., (*2011) Fig. (13).

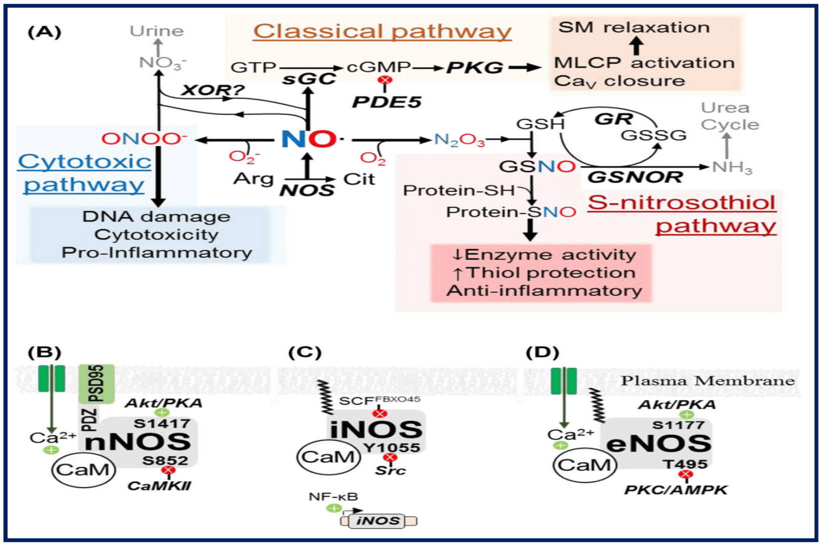

Fig. 13: Illustrates nitric oxide metabolism and regulation. (A) Intermediates, enzymes (bold, italics), and biochemical effects (shaded boxes) of classical, S-nitrosothiols, and cytotoxic NO signaling. Gray text and arrows indicate excretion pathways. Arg: arginine. Cit: citrulline. GR: GSH reductase. SM: smooth muscle. (B-D) Transcriptional and post-translational regulation of neuronal (B), inducible (C), and endothelial (D) nitric oxide synthase (NOS) isoforms. Kinases, phosphoregulatory sites, and inhibitory ubiquitin ligases are shown. Green +'s and red X's indicate positive and negative regulation, respectively.

NO is a nonpolar, selectively reactive gas with an unpaired electron. It reacts with ferrous (Fe2+) hemoglobin, molecular oxygen (O2), and superoxide (O2 −), respectively, to promote the three established NO signal transduction mechanisms: classical sGC-cGMP signaling, S-nitrosation, and the peroxynitrite (ONOO−) cytotoxic pathway Fig. (13).

Mostofa *et al.,* (2014) reported that application of a combination of exogenous GSH and SNP in Cu-treated O. sativa seedlings was found to ameliorate the effects of Cu toxicity through a reduction in levels of both lipid peroxidation and ROS-related enzymes. Different cotton genotypes pretreated with salicylic acid (SA) and ascorbic acid (AsA, vitamin C) were associated with a decrease in oxidative stress in Cu-treated plants and a lower level of toxicity under these conditions. SA participates in plant signalization with a marked effect on antioxidant enzymes, inhibiting their translocation Metwally *et al.,* (2003), whereas AsA regulates cellular processes like photosynthesis, cell expansion, root elongation, and transmembrane electron transport and causes marked exclusion and a decrease in Cu uptake Mei *et al*., (2015) Fig. (14).

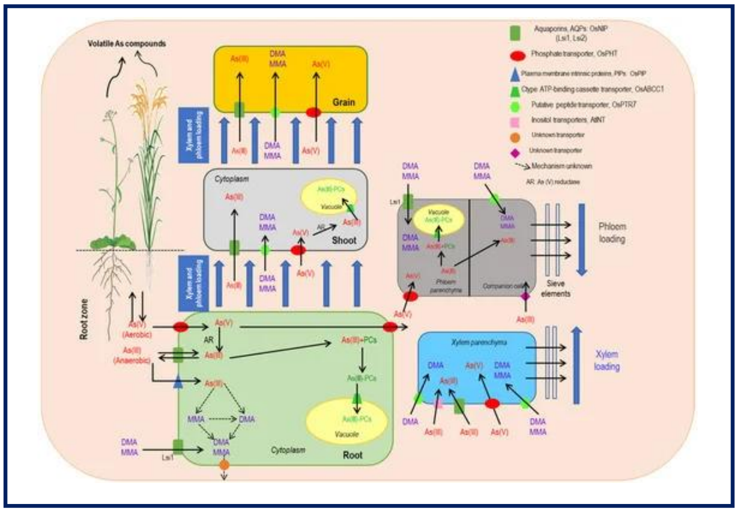

Fig. 14: Schematic illustration of As uptake, translocation, accumulation and detoxification in plants. The dotted arrows indicate that the pathways/mechanism are not known properly. MMA: monomethylarsinic acid [(CH3AsO (OH)2)]; DMA: dimethylarsinic acid [(CH3)2AsOOH)]; nodulin 26-like intrinsic proteins (NIPs)) which are as a group recognized as aquaporin channels (AQPs: OsNIP); OsPHT: phosphate transporter; PIPs: plasma membrane intrinsic proteins (OsPIP); OsABCC1: C type ATP-binding cassette transporter; OsPTR7: putative peptide transporter; AtINT: inositol transporters; AR: As (V) reductase. As (V) can be entered to the root through OsPHT. As (III) can be entered or to be excreted through AQPs/OsNIP. As (V) can be converted into As (III) by the activity of AR. As (III) can be bound to GSH to form PCs complex and sequestrated into vacuole. As (III) can also converted into organic DMA and MMA (but the mechanism is not known clearly), both of the organic forms can be excreted outside the cell through unknown transporter. DMA and MMA can also enter the cell trough AQPs/OsNIP. The AQPs/OsNIP, OsPHT and OsPTR7 have been assumed to be the transporter of various As species [As (III)/As (V)/MMA/DMA] towards the shoot and grain. Some of the As can also be released to the atmosphere as volatile As compounds. After: Nahar *et al., (*2022).

4.3. Role of Aluminium in plants

Aluminum (Al) is the third most abundant element overall, after silicon and oxygen, found in food, air, soil, and water., Al is solubilized into $[Al\ (H_2O)\ _6]^{3+}$ in which the Al^{3+} cation is highly toxic to many plant species and causes serious effects on plant growth particularly under acidic conditions Kochian *et al.,* (2015), Mattiello *et al.,* (2014). Toxicity of Aluminum (Al) is trisggered by acidic soils particularly at a low pH ($pH < 5.0$) Arunakumara *et al., (*2013) and causes direct inhibition of root elongation and interferes with plant nutrient uptake.

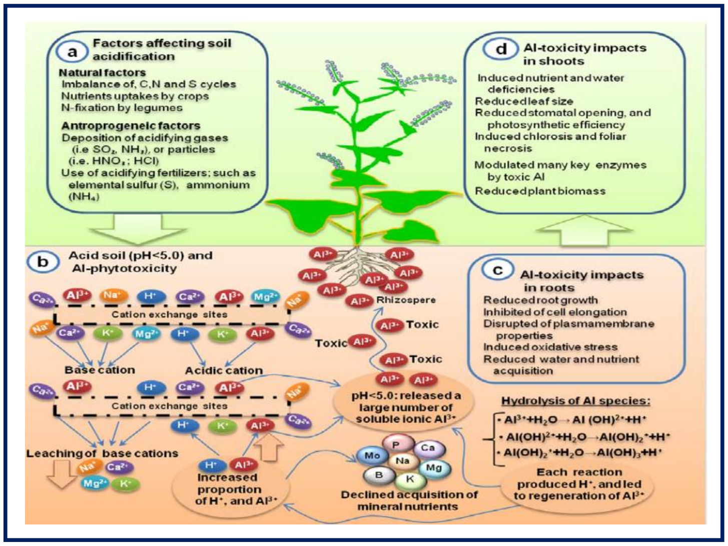

Fig. 15: Illustrates a general view of the factors affecting soil acidification, subsequent Al toxicity, and impacts in plants. (a) Natural and anthropogenic sources for occurring soil acidification. (b) Impact of cation saturation ratio in soil that led to increased exchangeable Al^{3+}, and reduce acquisition of mineral nutrients. (c) Consequence of Al toxicity in roots, and thereby (d) impact of Al toxicity in shoots. After Md. Atikur Rahman *et al., (*2018)

Atikur Rahman *et al., (*2018), stated that Soil acidification is an important factor that influences Al toxicity on agricultural land. A number of natural and/or anthropogenic processes Fig. (15) .Causingacidification of soil. Deposition of atmospheric gases or particles such as SO_2, NH_3, HNO_3, and HCl; and application of acidifying fertilizer including elemental sulfur (S) or ammonium (NH4) salt accelerated the soil acidification process that led to increased soluble Al^{3+} concentrations in the soil solution Goulding, (2016). Moreover, the imbalance of N, S, and C cycles, uptake of N by legumes, and intensified leaching of base cations (BC) were responsible for increasing H^{+} ions and decreasing soil pH level Bolan, *et al., (*1991). Over 100 years ago, it was noted for the first time that the concentration of soluble Al^{3+} increased in soils Veitch, (1904). Al^{3+} was able to create phytotoxicity in the rhizosphere when the pH was < 5. Most prominent sign of Al toxicity was considered casing inhibition of root growth Delhaize and Ryan, (1995) Soil pH is often considered a master variable as it controls solubility, bioavailability, mobility, ionic speciation, and ultimately toxicity of any metal in the soil Rengel, (2002). Ion availability in soil solution is influenced by low-pH. For example, Mn oxide solubilizes at soil pH below 5.5, and releases Mn^{2+} ions; at pH 4.3, a large amount of soluble Al^{3+} is released; at pH < 3.8, Fe becomes the exchangeable ion in the soil solution Chen and Liao, (2016), Delhaize and Ryan, (1995). The pH-dependent metal toxicity is quite complex; acid deposition to soil promotes soil acidity wherein more soluble ions are released into the soil solution. Consequently, potential phytotoxicity of metal ions was found to be enhanced due to their increased availability and concentration in soil solution Rengel, (2002). The Al^{+3} and Al (OH)$^{4-}$ are often described as the major rhizotoxicity Al species at low and high-PH levels, respectively. At low pH (about 4.3) soluble ionic aluminum (Al$^{3+)}$ is the most dominant form that is toxic for plant growth Bojórquez-Quintal *et al., (*2017). Surprisingly, it appears that toxic Al Acid rain/deposition has dramatic impacts on leachability of essential nutrient cations, mobility of toxic element (Al^{3+}), and acidity development in soil Driscoll, *et al.,* (2003). Basic and acidic cations are available at soil exchange sites or in the soil solution. Cation exchange sites that hold cations in the soil are negatively charged. Soil is buffered during acidification by a series of chemical processes resulting in the replacement of exchangeable base cations such as Ca^{2+}, Mg^{2+}, K^{+} , and Na^{+} by H^{+} and Al^{3+} at the cation exchange sites Goulding, (2016). Concurrently, the proportion of acidic cations such as H+ and Al^{3+} ^{i}n the soil solution increases. Often, acid rain stimulates the leaching of base cations such as Ca$^{2+,}$ Mg^{2+}, K^{+} , and Na^{+} from soil. Therefore, the essential nutrient cations such as Ca^{2+}, Mg^{2+}, and K^{+} are leached resulting in the depletion of base cations (BC) from the soil. The significant losses of these nutrient cations from soil solution or soil exchange sites result in nutrient imbalance in the soil. However, acid soils contain high amounts of Al^{3+} and a low amount of BC that are linked to deficiencies of important plant nutrients. Soil toxicity is known to be induced by the excess cations such as Mn^{2+}, Fe^{3+}, H^{+} and Al^{3+} Bojórquez-Quintal *et al.,* (2017).Among these, Al^{3+} is the most critical cation that leads to rhizotoxicity and severely impairs plant growth in acid soil. Brunner and Sperisen, (2013) stated that when the ratio of BC/Al^{3+} less than 1 in soil solution the potential index for the adverse effect of soluble Al^{3+} and nutrient imbalance for plant growth was considered . Nawaz, *et al., (*2012) reported that availability of BC and toxic Al^{3+} in acid soil depending on several factors such as acid rain, soil properties, cation exchange capacity (CEC), soil texture and initial base content in soil

Hence, it is considered as a primary limiting factor of plant growth and development in acidic soils as reported by Singh, *et al., (*2017), Pickar-Oliver and Gersbach, (2019). Due to highly extensively present in the Earth´s crust causing highly toxic effects in plants, recent reviews have already addressed the main aspects regarding the physiological, metabolic, and molecular regulation of its many effects in plant homeostasis. Some examples are shown in Yan, *et al., (*2021), Zhang, *et al., (*2021). Therefore, this section is limited to a general description of the main aspects of Al tolerance and exclusion machinery in plants. Soluble, element is converted to toxic forms that induce severe damage in plant roots, especially in non-tolerant ones. Al can induce stress in rice roots, leading to severe anatomical changes that include modifications to the length and diameter of xylem vessels, reductions in size of the metaxylem vessels and vascular bundles, and stomatal closure, which limits photosynthetic activity Samad *et al., (*2020). The increase and accumulation of ROS levels in plants leads to oxidative stress, reducing the levels of important antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), glutathione S-transferase (GST), and peroxidase. Additionally, Xu, *et al., (*2018) reported that prolonged effects of the oxidative state caused chromosomal aberrations and cell membrane peroxidation inducing negative effects on photosynthetic activity, damaging the cell structure, decreasing stomatal conductance, and, finally, leading to programmed cell death or apoptosis. Exclusion and tolerance are the two main strategies developed by plants during the course of evolution to overcome Al toxicity, whereby the plant cell prevents the entrance of Al into the roots (apoplast and symplast), while in the case of tolerance, Al is transported inside the cell where it can be sequestered into organelles and detoxified Kochian *et al., (*2015), Delhaize *et al., (*2012). This process includes the activation of various transporters such as the Al-activated malate transporter (ALMT) family (anion transport) and the multidrug and toxic compound extrusion (MATE) family (OA/H+ antiport transport), which aid the cell in the liberation of OAs (citrate, malate, oxalate, phenols, and polypeptides through roots into the soil acting as ligands to chelate Al ions, forming stable complexes) into the rhizosphere to avoid the entrance of Al into the plant cell Riaz *et al., (*2018) , Takanashi *et al., (*2014). Once inside the cell, the metal–OA complexes can be accumulated in vacuoles with the intervention of carrier molecules such as phytochelatins (PC) and metallothionein (MTs). Al translocation and accumulation are possible in a very narrow group of plants such as common tea (Camellia sinensis), hydrangea (Hydrangea L), buckwheat (Fagopyrum esculentum), and Melastoma malabatricum. These plants have the capability to accumulate above Al concentrations of 1000–3000 mg/kg or higher Kochian, *et al., (*2015). A different way of exerting Al tolerance is through mediation by other protein complexes formed by ABC transporters that are sensitive to Al rhizotoxicity: STAR1 and STAR2. They also participate in UDP–glucose efflux into the cell wall, modifying its composition and decreasing the capacity of Al to bind to the cell wall Xia *et al., (*2010). In fact, studies on non-model plant systems, such as Andropogon virginicus L., have revealed that ABCG type transporters are colocalize in roots and leaves with Al absorption areas. Specifically, the expression of such proteins has been observed in cell membranes, root endo- and exodermis, and the vascular bundle sheath and epidermal cell layers, thus indicating their possible role in Al-accumulation in plants Zhang *et al., (*2021). Likewise, our research group reported a $FeALS_3$ sequence that is involved in Al tolerance in buckwheat Reyna-Llorens *et al., (*2015). Gene expression was found to be constitutive and increased when the Al concentration was augmented. Interestingly, increasing levels of abscisic acid (ABA) were correlated with an increase in $FeALS_3$ expression, suggesting a role for these phytohormones in Al tolerance in F. esculentum Reyna-Llorens *et al., (*2015). Recently, it has been demonstrated that, after the first 48 h of exposure to the threshold Al^{3+} concentration (50 μM) in buckwheat, the levels of important antioxidant enzymes increase along with the ABA levels, implying that they might participate in root recovery mechanisms Salazar-Chavarría *et al., (*2020). Other elements and phytochemical compounds play roles in Al tolerance mechanisms. For instance, elements such as magnesium (Mg) can act by displacing/competing with Al for binding sites within root cells; or by increasing citrate exudation, influencing the upregulation of MATE-like genes Xia *et al., (*2010). In Camellia sinensis, a recent study indicated that phytochemical compounds such as epigallocatechin gallate and polymeric proanthocyanidins were detected colocalize in the same tissues with high Al accumulation, roots, and old leaves. These polyphenols can form complexes with Al, demonstrating their roles in the high accumulation capacity exhibited by tea plants Fu *et al., (*2020). The implication of phenolic substances has already been described in other plant systems such as Eucalyptus camaldulensis Tahara, *et al., (*2014).

4.4. Role of Lead in Plants

Kanwal, *et al., (*2014) stated that in global system, there has been a trend for a continuous escalation in the release of pollutants such as Pb, and many ecosystems have been affected lead. Herbette, *et al.,* (2006) reported that pollutants by lead described as a serious problem for different plant species, which is not a part of any metabolic pathway, in addition low concentrations can be considered as a toxic. Kohli, *et al.,* (2019), Uzu, *et al.,* (2010) reported that lead can be translocated to the shoots after its absorption into the roots through passive absorption mechanisms that rely on H+/ATPase systems; and then translocated via apoplast through the endodermis (which acts as a natural barrier in deeper tissues, such as the stele) and then transported via symplast to vascular tissues Fig.(16).

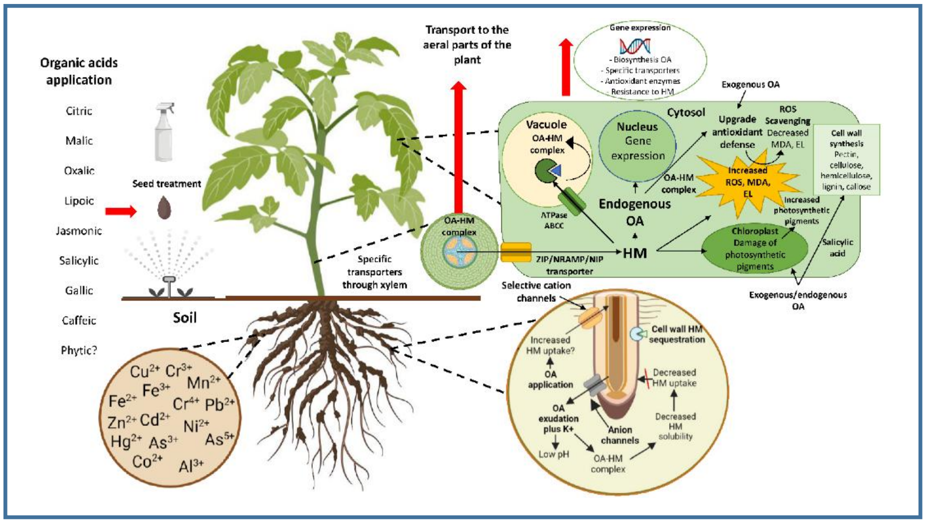

Fig. 16: Schematic representation of the physiological and molecular processes of absorption/translocation of metals into plants. After Vega *et al.* (2022)

Lead element affects many of physiological characteristics, creating a growth impairment, with subsequent effects on the proper development of roots (swelling and stunted growth), seeds, and seedlings, increasing the presence of necrotic lesions, causing leaf chlorosis, reducing the seed germination rate, decreasing the root/stem biomass, and altering the water status, mineral nutrition, and enzymatic activity Kohli *et al., (*2019).One of the most profound effects is observed in the overall plant photosynthetic machinery Kaur, *et al., (*2014), where the electron transport processes are disrupted, causing a four- to five-fold decrease in the energy transformation efficiency of photosystem II (e.g., as registered in wheat) Rizvi *et al., (*2020), Kaur *et al., (*2014), Madhu *et al., (*2020) Fig.(17). Plants in contact with Pb respond in different ways depending on the ion concentration, level of exposure, and the plant's developmental stage; however, when Pb levels are low, the plant can adapt to the conditions Gupta *et al., (*2009).

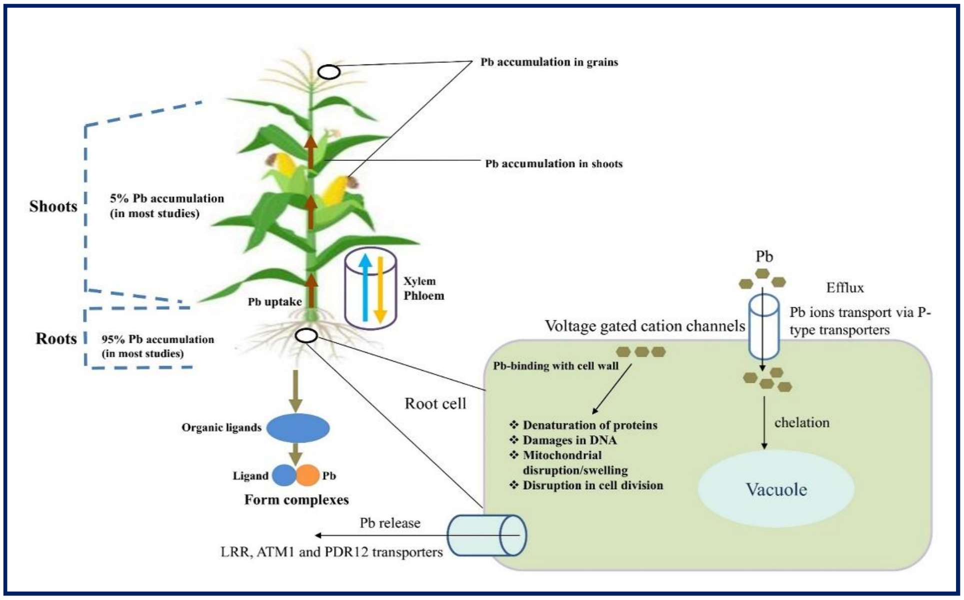

Fig. 17: Potential uptake mechanisms and accumulation of lead (Pb) in plant parts. The sequence of Pb accumulation in different organs of cereals particularly in wheat is as; roots > shoots > shells > grains. Relatively higher Pb accumulation in root tissues could be an inactivate Pb in root cell walls. However, accumulation of Pb in grain is of main concern regarding its entry in food chain. Bio concentration factor (BCF) and translocation factor (TF) are very important characteristics to be focused regarding accumulation and translocation of Pb. The heavy-metal mobility factor (MF) is equal to the ratio of the sum of labile fractions (exchangeable and bound-to-carbonate fractions) to the sum of all fractions, which is a good index to describe the relative mobility and bioavailable form of the metals in soils. After: Muhammad Aslam *et al., (*2020)

An active part of soil, numerous organic compounds and root exudates Jones *et al., (*2009), directly affect the rhizosphere. For example, 10–40% of the plants' (organic and inorganic) photosynthetically fixed carbon is released in this part of the soil McNear, (2013). Mucilage sloughed off root cap, boundary cells, and exudates constitute the rhizodeposition. Mucilage assists in soil lubrication, root defense from desiccation, soil quality improvement, and nutrient uptake during root tip development McNear, (2013). In the availability and absorption of metals by plants, the rhizosphere and soil microorganisms play a key role. By catalyzing the redox reaction, microbial activity alters the trend of HM uptake process Dinh *et al.,* (2020). The microenvironment formed by various discharged compounds contributes to the toxicity of HMs in nutrient absorption, including Pb as tested in Jitendra *et al., (*2017). Root exudates consist of compounds of low and high molecular weight that are released actively and passively. Components of low molecular weight help to attract and use soil biota, which promote the rhizosphere through colonization or symbiosis on roots Hawes *et al., (*2002). In inter- and intraplant interactions, root exudates play a role, helping to signal events Kumar and Bais, (2012). The important micronutrients in metallic soils become accessible to plant roots due to the discharge of metal chelators. By improving their mobility and solubility, these chelators enhance the bioavailability of metals, and this is achieved by breaking the bonds between metals and soil particles Rao *et al.,* (2018). Lead, widely available in the plant rhizosphere, has poor bioavailability for plants to be absorbed as it precipitates as sulfates and phosphates Blaylock and Huang, (2000). Furthermore, the translocation of Pb is restricted by the roots, which accumulate maximum Pb contents. As recently reported by Li, *et al., (*2020), the bioavailability of Pb depends on its concentration in the soil, the physical and chemical state of the soil, and the particular genotype of specific plant species. Lead mobility is strongly influenced by soil pH levels, i.e., increased mobility and Pb absorption has been recorded at low pH soils (3.9). Isotopes labeling techniques showed that more than 90% of Pb produced from ryegrass and wheat passed through the atmosphere Alexander *et al.,* (2006). In the cell wall or in the form of extracellular precipitates on root tissues, much of the absorbed Pb occurs as bound to exchangeable ion sites Sahi *et al.,* (2002). For Pb movement under low concentration in roots, the endodermis acts as a partial barrier. Lead ions in the case of wheat roots can be extracted by using citric acid Xie *et al., (*2018). After getting into the root cortex, Pb ions transfer to the apoplastic space through the conductive transpiration system. Furthermore, it gives symplastic access to the region of lateral root initiation and young roots that grow. Cross-membrane movement within the cytoplasm and membrane protein Dong *et al.,* (2009), regulates its mobility. Transporters that are present in xylem parenchyma cells or phloem companion cells primarily facilitate the long-distance transport of Pb from roots to shoots Dong *et al.,* (2009). The transport of Pb occurs from the soil into root epidermal cells, followed by loading into the root xylem vessels for distribution into other plant organs. All plant transporter proteins are membrane proteins with Pb homeostasis as their responsibility Romanowska *et al., (*2012). Vacuole sequestration potential (VSC) also plays a major role in the transport and sequestration of metals over long distances Williams *et al., (*2000). Via cooperation, tonoplast-localized transporters and ion chelators automatically change the available metal ions in the surrounding region Peng and Gong, (2014), Fig. (17).

Translocation/transport phenomena of Pb slightly differ from other HMs. Normally, 5% of Pb is transported into aerial components Kiran and Prasad, (2017) and 95% remains accumulated in roots Chandra, *et al., (*2018). The possible mechanism is that in plant roots, ion-transferable cell wall sites mediate extracellular Pb binding. In this way, with the carboxyl group, Pb forms stable binding complexes and remains located in the roots. The components of the cell wall, such as glucuronic acid, limit apoplastic transport into the above plant components Inoue, *et al., (*2013). P-type transporters or Pb cellular complexes that decrease the toxicity of Pb by endorsing sequestration into a specific organelle Jiang, *et al., (*2017) regulate lead efflux. Previous studies have indicated that Leucine-rich repeat (LRR), ATM1, and PDR12 the transporters may be associated with cell cellular Pb extrusion Zhu, *et al., (*2013).

Lead (Pb) tolerance mechanisms described in plants, we can consider (**a**) eliminating Pb through cell wall pumps; (**b**) uptake reduction; (**c**) chelation with thiol compounds in the cytosol with the aid of PCs and MTs; (**d**) sequestration and inactivation in organelles (vacuoles); and (**e**) detoxification of Pb-induced ROS generation Kaur, *et al., (*2015), Usman, *et al., (*2020), Pereira, *et al., (*2017). On the other hand, prominent levels of this element cause stimulate ROS production and plants lack the ability to overcome this event Kaur *et al., (*2015). This also produces an upregulation of genes that code for enzymes that contribute to this process, such as glutathione reductase, GST, ascorbate peroxidase, and SOD Usman *et al.,* (2020). Pb also triggers modifications to leaves in sensitive plants, such as thylakoidal membrane disorganization, alterations to chloroplast morphology, nuclear membrane disruption, and the formation of electrodense deposits Pereira *et al., (*2017). In resistant plants, interactions with Pb were shown to modify the structure of mitochondria and cause nuclear membrane disruption in root cells Reis *et al.,* (2015).

4.5. Role of Cadmium (Cd) in Plants

Grant *et al.* (1998) reported that cadmium element is very soluble in water with a long half-life; therefore, it accumulates in soil and is potentially toxic to plants. Due to adsorption by plant, it is a risk to plants used for human or animal consumption. Higher Cd concentrations can be toxic to plants, especially in roots, where it can be absorbed into the rhizodermis and root cortex, either through apoplastic or symplastic pathways, and then through the plasma membrane of the endodermis, before entering the stele for long-distance transport. This metal can be readily absorbed and sequestered into root vacuoles or transported into the xylem to be distributed along the entire plant. Accumulation of cadmium (Cd) is greater in roots comparing with the other parts of plant Kushwaha *et al.* (2016), Ismael *et al.* (2019). Bayçu *et al.* (2016) reported that as with many other toxic metals/metalloids, high Cd concentrations in plants cause toxicity at the physiological, morphological, and molecular levels and can affect important cellular mechanisms. That causing an overall decrease in plant growth, changes in bioavailability of nutrient uptake and changes in the photosynthetic machinery Gallego etal (2012), Jakubowska *et al.* (2015) Rizwan *et al.* (2018), Murtaza *et al.* (2016).Murtaza *et al.* (2016) they stated that cadmium stress are the main plant physiological responses to reducethe root length and growth. Brunetti *et al.* (2015) reported that in A. thaliana, Cd could also induces the expression of transport genes such as AtABCC3, when upregulated and can rescue the phenotype in an atabcc1 atabcc2 double knockout mutant under conditions of Cd toxicity. Highest AtABCC3 levels were observed when Cd concentrations were also high, indicating that this gene is modulated by an increase in the Cd concentration. Heyno *et al.* (2008), Janik *et al.* (2010) reported that Cd could compete with essential metallic elements such as Zn, Ca, and Fe for transport, creating mineral deficiencies, furthermore interrupting the activity of important enzymes, and thereby, inhibiting the flow of electrons that can react with oxygen and deplete the pool of reduced glutathione due to its elevated affinity to thiol groups. In A. thaliana and A. halleri, HMA4 and NAS2 (Nicotianamine Synthase 2) participate in the translocation of both Cd and Zn from the roots to the shoots. The former codes for a heavy metal ATPase, while the latter helps to increase the level of nicotinic acid, which plays an important role in metal/metalloid homeostasis Li *et al.* (2017). Cd also induces adaptative response (AR) through metabolic blockers of protein kinase cascades, DNA repair, oxidative stress, and de novo translation Chakrabarti and Mukherjee (2021). Shiyu *et al.* (2020) stated that mechanisms of Cd tolerance involve **(a)** reducing its absorption and transport from roots to shoots; **(b)** compartmentation in the cell wall and chelation in root cell vacuoles; **(c)** enhancing the concentration of antioxidants and ant oxidation enzymatic activity; and **(d)** upregulating the synthesis of PC and changing the expression of heavy metal transporter genes .

4.6. Role of boron in Plants

Boron (B) is a micronutrient critical to the growth and health of all crops. It is a component of plant cell walls and reproductive structures. It is a mobile nutrient within the soil, meaning it is prone to movement within the soil. Because it is required in small amounts, it is important to deliver B as evenly as possible across the field. Traditional fertilizer blends containing B struggle to achieve uniform nutrient distribution. Despite the need for this critical nutrient, B is the second most widespread micronutrient deficiency problem worldwide after zinc. Boron plays a key role in a diverse range of plant functions including cell wall formation and stability, maintenance of structural and functional integrity of biological membranes, movement of sugar or energy into growing parts of plants, and pollination and seed set Fig. (18).

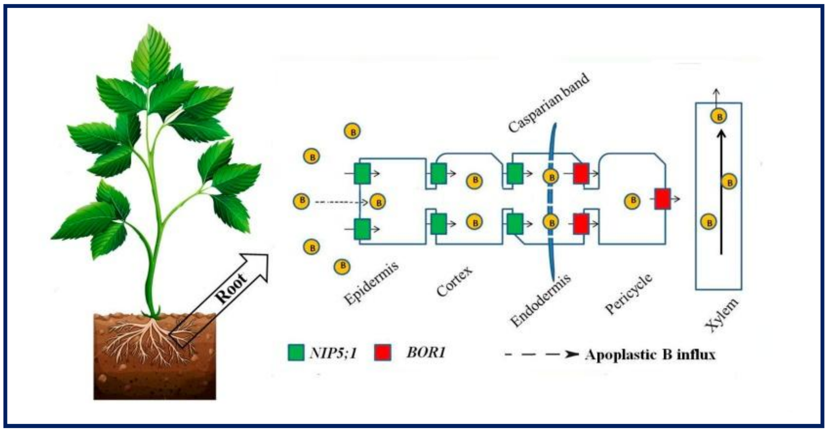

Fig. 18: Illustrates mechanism of boron uptake and transport in plants under limited B conditions. Modified from Takano *et al., (*2008), Abou seeda *et al., (*2021)

Adequate of boron (B) is also required for effective nitrogen fixation and nodulation in legume crops. Boron deficiency commonly results in empty pollen grains, poor pollen vitality and a reduced number of flowers per plant. Low B supply can also stunt root growth.

According to some researches, there are three main routes of boron (B) entry into plant cells;

(a) Passive, bidirectional diffusion via lipid bilayer: Phospholipid bilayers are known to be highly permeable to B Reid, (2014).

(b) ii. Passive bidirectional diffusion via selective or non-selective channels:

Reports suggest a parallel pathway in the plasma membranes involving membrane channels that facilitate the movement of B in plants Reid, (2014).

(c) . Active extrusion pumping: In spite of the rapid B entry into theplant cells, some plant tissues are found to have the capability to maintain low internal B concentration and the concentration is below that of the external medium Reid, (2014). Forinstance, the B-tolerant barley cultivar "Sahara" can maintain the lower internal concentration of B in comparison to the surrounding external solutions Hayes and Reid, (2004); Reid, (2014). In the presence of metabolic inhibitors, the generation of a concentration gradient across the plasma membrane is lost, and this showed that energy input is essential to maintain it. At present, in the case of various plant and tissue types, the identities of active efflux transporters have been authenticated. To establish the concentration gradients, these transporters show their dependency on two aspects. First, the rate at which B can be pumped out and secondly, how B can escape back when it passes via the lipid bilayer and channels Reid, (2014). Boron is exported into and out of the cell in the form of uncharged boric acid Zangi and Filella, (2012). In soils of arid regions, high concentrations of B are found naturally Nable *et al.,* (1997); Rees *et al.,* (2011), whereas anthropogenic activities such as irrigation with B-laden water, deposition of fly ash or coal mining also results from the increased deposition of B in soils Nable *et al.,* (1997); Parks and Edwards, (2005); Rees, *et al.,* (2011). Plants uptake B from the soil through roots and it is translocated to the stem and ultimately to the leaves via the transpiration stream Rees *et al.,* (2011); Schulin, Johnson & Frossard, (2010) Fig. (19). B uptake requires the involvement of both channels (NIP5;1) and transporters (BOR1), responsible for xylem loading Miwa and Fujiwara, 2010). Protein channels facilitate the efflux, and it has been revealed thatthis efflux provides tolerance to plants against higher levels of B, which may cause toxicity Hayes and Reid, (2004); Zangi and Filella, (2012) Fig. (20). It has been established that the extrusion of B is an active transport, although its transport is done in the form of B (OH) Zangi and Filella, (2012). The accumulation of B differs significantly among different organs of a plant Oertli, (1994); Rees *et al.,* (2011).

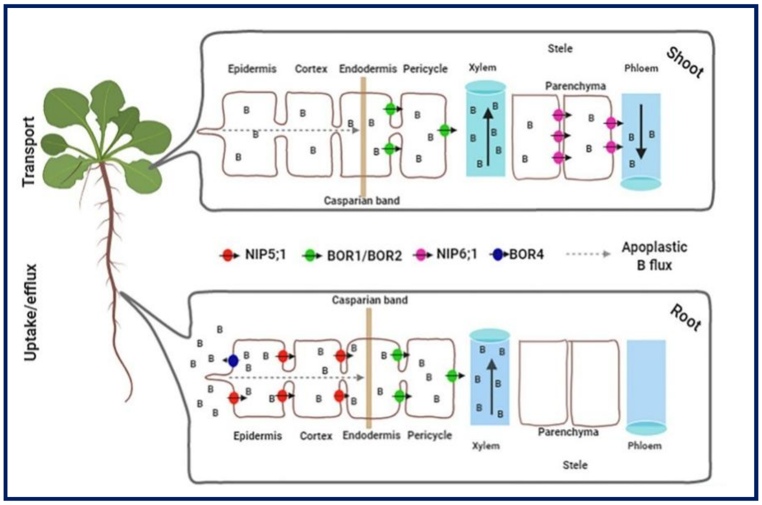

Fig. 19: Illustrates homeostasis of the boron (B) levels in plant cell mediated by transports. In Arabidopsis thaliana roots, B homeostasis is mainly based on three transport mechanisms across the plasma membrane. The first is the simple diffusion of boric acid (H_3BO_3), without charge through the lipid bilayers. The second mechanism represents the facilitated diffusion mediated by channels of the aquaporin family, such as NIP5;1. The third refers to the B movement by specific transports (e.g., BOR 1, BOR2, and BOR4). The uptake channels NIP5;1 is expressed in the plasma membranes of root cap and epidermal cells with outside/soilfacing polarity NIP5;1 mediates the efficient radial transport of B from the soil through the epidermis and cortex to the endoderm. The Casparian band developed in the endoderm limits the apoplastic flow of B to the stele. BOR1 and BOR2 are expressed at the endodermis in meristematic and maturation zones. BOR1 and BOR2 are polarly localized in the stele-side plasma membrane domain. BOR4 located in the root epidermis aid in the efflux of B from the root to the soil solution. In shoots, NIP6;1 is necessary for the transport of B from xylem to phloem in nodal regions, being located in the parenchyma of the stele Figures were created using the software biorender (app.biorender.com). After Pereira *et al., (*2021).

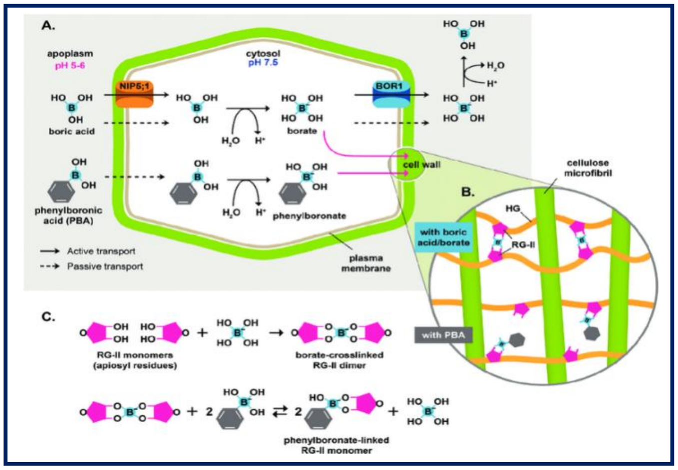

Fig. 20: Illustrates Boric acid (BA)/phenylboronic acid (PBA) uptake into plant cells. (A) Passive and active uptake mechanisms of BA and PBA through either diffusion or the NIP5;1 channel protein. Due to the cytosolic pH, BA and PBA are diverted into borate and phenylboronate anions, which react with the apiosyl residues of rhamnogalacturonan-II (RG-II) in the cell wall. Export of borate and phenylboronate out of a plant cell occurs via diffusion or the BOR1 export transporter. (B) Close-up of a cell wall pectin matrix with borate cross-linking two RG-II monomers (only the apiosyl residues are shown for simplicity) and phenylboronate interfering with the cross-linking by competitively binding to only one RG-II monomer. (C) Reaction of the borate anion and the phenylboronate anion with apiosyl residues of RG-II monomers.After Matthes etal (2020).

4.6.1. Boron transporter

Previously, two transporters viz. AtNIP 5;1 and AtBOR1 were reported to be involved in B uptake in Arabidopsis Takano, *et al.,* (2002), (2006). In rice, OsBOR1, a homologue of AtBOR1, was shown to participate in the uptake of B and, in addition to this, in xylem loading; OsBOR1 is expressed in the root exodermis, endodermis, and the stele Nakagawa *et al.,* (2007) Figs.21 and 22).

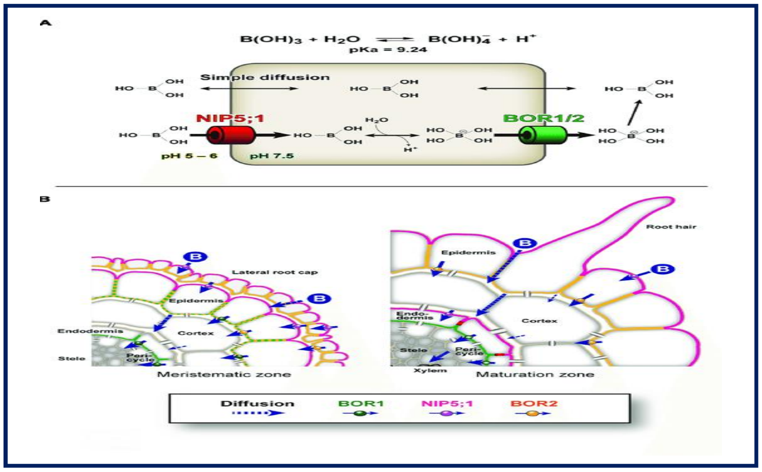

Fig. 21: Models of Boron transport pathways. (A) Boron (B) transport across the plasma membrane. Boron transport and homeostasis are primarily based on three transport mechanisms across the plasma membrane (PM). The first is simple diffusion of uncharged boric acid across lipid bilayers. The second is facilitated diffusion of boric acid via NIP II boric acid channels, e.g., Arabidopsis NIP5;1. The third is export of borate via borate transporters, e.g., Arabidopsis BOR1 and BOR2. The boric acid channels transport boric acid into cells under physiological conditions. In the cytoplasm, which has a relatively high pH, boric acid is dissociated to borate anion and exported by borate uniporters driven by the electrochemical gradient. In the apoplast, which has a low pH, borate anion is rapidly converted to boric

acid, and thus BORs can generate an uphill gradient of boric acid. (B) Cell-type specific expression patterns of NIP5;1, BOR1, and BOR2 in Arabidopsis roots under low-B conditions. NIP5;1 is expressed in lateral root cap and epidermis in the meristematic zone and epidermis and endodermis in the maturation zone (Wang *et al.,* 2017).BOR1 is expressed in epidermis in meristem and endodermis in both meristematic and maturation zones (Yoshinari *et al.,* 2016). BOR2 is expressed in lateral root cap and epidermis in both meristematic and maturation zones (Miwa *et al.,* 2013). NIP5;1 is polarly localized in the soil-side PM domain (Takano *et al.,* 2010). BOR1 and BOR2 are polarly localized in the stele-side PM domain (Takano *et al.,* 2010; Miwa *et al.,* 2013). The PM of endodermal cells is separated by the Casparian strip domain (Alassimone *et al.,* 2010), and NIP5;1 and BOR1 are strictly separated to the two domains. Boric acid/borate is transported transcellulary from the soil to the xylem. In mature portions of roots, BOR1 at the stele side of endodermal cells is responsible for keeping boric acid/borate in the apoplasm in the stele.After Akira Yoshinari† and Junpei Takano (2017).

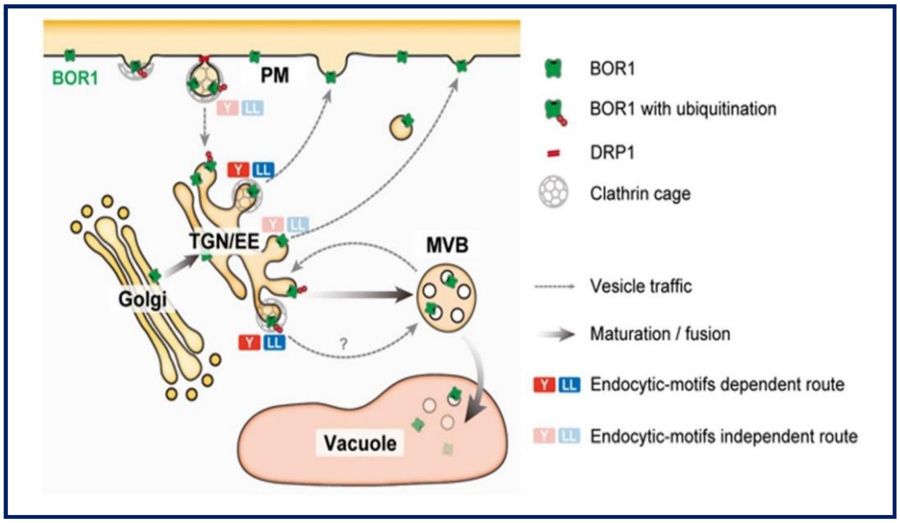

Fig. 22: Illustrates a model of post-Golgi trafficking of BOR1. BOR1 is internalized through clathrin and DRP1-dependent endocytosis and transported to the trans-Golgi network/early endosome (TGN/EE). Ubiquitinated BOR1 is sorted to intraluminal vesicles of multi-vesicular bodies (MVBs) by the endosomal sorting complexes required for transport (ESCRT) machinery. MVBs containing BOR1 fuse with the vacuole, releasing intraluminal vesicles. In the vacuole, BOR1 is immediately degraded by proteases. Unubiquitinated BOR1 is recycled to the PM from the TGN/EE via a clathrin-dependent or -independent route. BOR1 has endocytic motifs; three putative tyrosine motifs and a dileucine motif in the cytosolic loop region. These endocytic motifs bind to adaptor protein complexes involved in clathrin-dependent vesicle formation at the PM and TGN/EE. BOR1 variants lacking either motif did not show polar localization or B-induced vacuolar transport, although these variants were normally endocytosed under low B conditions Takano *et al.,* (2010); Wakuta *et al.,* (2015). These results suggest that the endocytic motifs of BOR1, rather than endocytosis are involved in polar recycling and vacuolar sorting of B from the TGN. After Yoshinari Akira and Junpei Takano (2017).

However, knockout of this gene in the shoot has resulted in significantly reduced B levels Nakagawa *et al.,* (2007). An influx transporter for B is AtNIP 5;1, which is known to transfer B from soil to the cells of the root in rice; however, OsBOR1 is known to be an efflux transporter for B Sasaki, etal, (2016). Several B transporters and aquaporins have been reported in different plants viz. AtTIP5 in Arabidopsis, OsBOR1-4, OsPIP2;4 and OsPIP2;7 in rice, HvBot1, HvNIP2;1 in barley; ZmBot1 in maize; TaBOR1 in wheat (Kumar *et al.,* (2014); Pang *et al.,* (2010); Reid, (2014);Wakuta *et al.* (2016); Yıldırım, (2017). OsNIP 3;1 is confined to the plasma membrane, it shows permeability to boric acid, and it is the closest homologue of AtNIP5;1. Hanaoka, etal (2014) noticed that OsNIP3;1 is expressed in both roots and shoots, and knock-out lines were not significantly affected in B uptake Sasaki *et al.,* (2016). In root exodermal cells and in the nodal region of adult leaves, OsNIP3;1/DTE1 is expressed at high levels, but its expression was enhanced by B shortage Liu *et al.,* (2015); Sasaki *et al.,* (2016).

However, the amount of B in the shoot of the dte1 mutant did not differ from the wild type; however, growth and total B content declined remarkably in the mutant lines Liu *et al.,* (2015); Sasaki *et al.,* (2016). Hence, similar to the Lsi1-Lsi2 Si uptake system in rice, OsNIP 3;1/DTE1, and OsBOR1 may represent a cooperative uptake system Sasaki *et al.,* (2016).

4.7. Role of Silicon in Plants

Silicon (Si) is the second most prevalent element in the Earth's crust; however, plants uptake Si only in the form of silicic acid, which is rare in most of the cultivated soils Deshmukh and Bélanger, (2016); Deshmukh et al., (2017); Ma *et al.,* (2006). With respect to Si accumulation in their tissues, plants are classified into accumulators, excluders and intermediate-types Mitani and Ma, (2005). The roots and shoots of different plants accumulate varying levels of Si in the form of amorphous silica (SiO2) and this variation is related to the uptake and transport of the metalloid in plants Deshmukh *et al.* (2020); Hodson *et al.,* (2005); Imtiaz *et al.,* (2016); Ma *et al.,* (2006). Katz *et al.* (2021) reported that several transporters and genes that are involved in Si uptake and accumulation have been studied so far. Although the study of Si transporters focuses on rice and other grasses (as is commonly the case in plant Si research Putra *et al.* (2020), Katz, (2014), the first plant gene to regulate Si accumulation was discovered in the gourd Cucurbita (Cucurbitaceae), regulating Si and phytoliths formation in the fruit rind Piperno *et al.* (2002) Fig. (23). Shortly after, a surge of discoveries of the physiology and genetics of Si uptake in grasses has arisen, revolving around the four Lsi transporters, all belonging to the NIP aquaporin family.

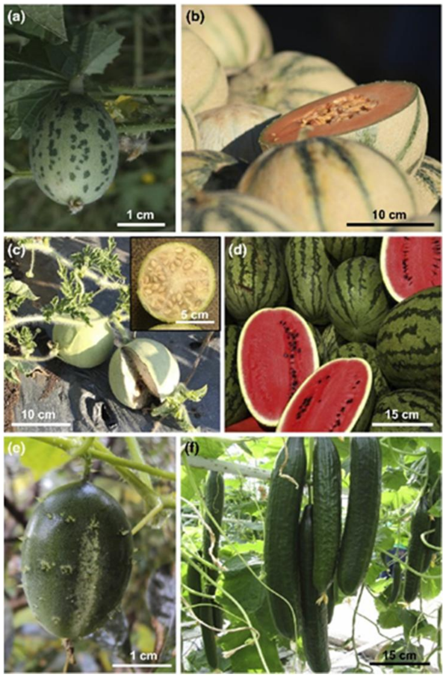

Fig. 23: Cucurbitaceae crops and their wild progenitor to illustrate the domestication syndrome. **(a, b)** Honey melon (Cucumis melo). (a) Wild melon progenitor, Asian agrestis (Cucumis melo subsp. melo f. agrestis). **(b)** Domesticated melon (Asian lineage). **(c, d)** Watermelon (Citrullus lanatus). **(c)**Wild watermelon progenitor, Kordofan melon (Citrullus lanatus subsp. cordophanus). **(d)** Domesticated watermelon. **(e, f)** Cucumber (Cucumis sativus). **(e)** Wild cucumber progenitor (**C**. sativus **f.** hardwickii). **(f)** Domesticated cucumber. Photographs credited to: **(a)** Balkar Singh; **(c)** Harry Paris; **(b, d, f)** Creative commons**; (e)** Hanno Schaefer. After Chomicki *et al.* (2019)

The first transporter to be discovered was the influx transporter Lsi1, located in the distal plasma membrane of root exodermis and endodermis cells Ma et al. (2006)]. An efflux transporter on the proximal plasma membrane of the same cells, Lsi2, transports system of Si uptake and distribution in grasses, with some variations in the details of where exactly each transporter is localized within each species Ma *et al.* (2008); Ma and Yamaji, (2015); Yan *et al.* (2018)] Fig.(24).

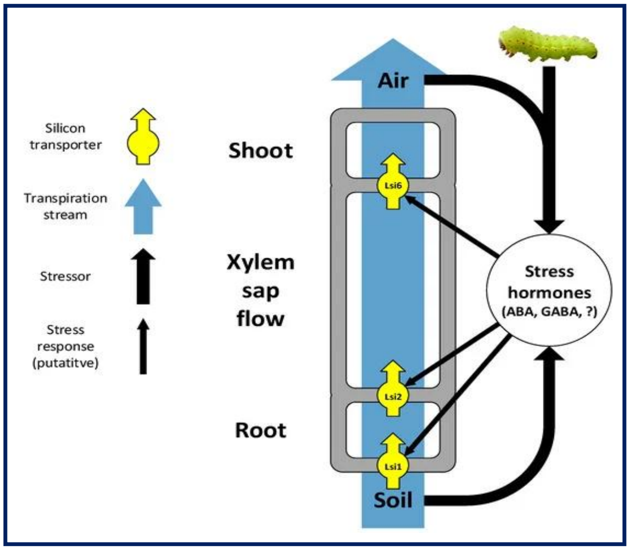

Fig. 24: A simplified model of Si uptake from the soil to the shoot through the transpiration stream, including main transporters and responses to external factors.
After Katz et al. (2021)

Si from the exodermis to the cortex and further loads it from the endodermis onto the xylem Ma, *et al.* (2007). A third transporter, Lsi6, exists in the shoots and is responsible for xylem offloading Yamaji *et al.* (2015).In grass shoot nodes, Lsi6 and Lsi3 (previously thought to be Lsi2 due to structural similarities) are involved in distributing Si among branches Yamaji *et al.* (2015), Yan *et al.* (2021). Lsi1 and Lsi6 transporters were also identified in the soybean Glycine max Deshmukh *et al.* (2013).In the Cucurbitaceae, a Si-accumulating dicotyledonous family, Lsi1 was also identified in all root cells of Cucurbita Mitan *et al*. (2011),Wang *et al.,* (2015) identified two putative Si transporters in cucumber (Cucumis) of the same family. Together with the early-identified gene responsible for Si accumulation in Cucurbita rinds Piperno *et al.* (2002), these studies suggest that Si transport systems in grasses and dicotyledons share some similarities. The recent identification of a gene regulating Si uptake by the mangrove Rhizophora apiculate without identifying the transporter itself Sahebi *et al.* (2014). Multiple genes regulating Si uptake and accumulation were also found in the horsetail Equisetum arvense Grégoire *et al.* (2012). Finally, it appears that Lsi-like genes that govern Si uptake are common in many groups of land plants, suggesting that the origins of these mechanisms are as ancient as the origins of land plants Trembath-Reichert *et al.* (2015). These findings further suggest that the physiology and genetics of Si transporters in non-grass species are only beginning to reveal themselves. Expression of the Lsi1 gene in rice is downregulated by Si supply, dehydration stress and abscisic acid (more strongly in Si-depleted plants), suggesting regulation of active Si uptake in response to changes in the transpiration stream and plant internal water balance Yamaji and Ma (2007). Further studies have demonstrated how plant hormones Kumar *et al.,* (2017) and internal Si and metal concentrations Chaiwong *et al.* (2020), Bokor *et al.* (2015) regulate the expression of Lsi1, Lsi2 and Lsi6 genes.

Rice is a well-known Si accumulator and its uptake mechanisms have been extensively studied Bhat *et al.,* (2019), Zargar *et al.,* (2019). However, the most puzzling question concerns the benefits that plants can derive from Si supplementation Mandlik *et al.,* (2020). Broadly, the higher benefits have been observed in those plant species that can uptake a higher amount of Si. However, some species belonging to the Solanaceae family, namely tomato, are considered excluders and yet they benefit from Si supplementation Heine *et al.,* (2005), Hoffmann *et al.* (2020). These pieces of evidence may be related to the changes that Si supplementation can exert and to the impact of soil properties. This is more evident with studies performed to evaluate the effect of Si supplementation on heavy metal tolerance Bhat *et al.,* (2019). Because of its practical benefits to plants, the International Plant Nutrition Institute now considers Si as a quasiessential element for plant growth. Silicic acid occurring in its monomeric form as H_4SiO_4 and this H_4SiO_4 is the plant available form of Si (PAS) present in soil Tubana *et al.,* (2016). PAS considerably affects the amount of Si accumulation in plants. Recently, an extensive study performed on different soil types has shown a strong positive correlation between PAS present in the soil and Si accumulation in the soybean leaves Deshmukh *et al.,* (2020). In the experiment performed by Deshmukh et al. (2020), soybean plants grown on soil containing <20 ppm Si were found to accumulate about 0.4% Si in leaves, whereas Si reached nearly 1% when the PAS concentration was high (>60 ppm) in the soil. In rice, Casparian strips present in the endodermis of roots block the apoplastic pathway of silicic acid and determine the symplastic pathway until stele Mandlik *et al.,* (2020). In the xylem cells, the level of Si reaches up to 18 mM Mitani et al. (2005). For instance, the concentration of Si in the xylem sap of rice cultured in a growth medium containing 0.5 mM Si reached 6 mM within 30 min and then it increased to 18 mM after 8.5 hrs. Mitani *et al.,* (2005). This is considered as one of the most puzzling questions about Si uptake in plants, because monosilicic acid starts polymerizing when the concentration exceeds 2 mM Ma and Yamaji, (2006). To date, how the concentration of Si reaches 18 mM without beingpolymerized is not yet known. The role of organic compounds that may form complexes with Si and thereby prevent polymerization has been suggested Mandlik *et al.,* (2020). The excess concentration of silicic acid present in the xylem sap is rapidly transported into the leaves where it begins to polymerize and is deposited as silica. In the leaf blade of rice, silicic acid undergoes polymerization and it forms a double-layer of Si beneath the cuticle, which helps to regulate transpiration Ma and Yamaji, (2006). Similarly, culm wall thickness as well as the size of vascular bundle of rice plant are increased by Si deposition and it provides strength to the stems Ma, *et al.,* (2001); Shimoyama, (1958). Silicon is deposited only in bulliform cells of the young leaves and as the plant matures, Si deposition increases and is detected in almost all cells Guerriero, *et al.* (2018); Sangster *et al.* (2001).

Several researchers Bauer *et al.,* (2011); He *et al.,* (2013), Hodson, (2016), reported that silica is deposited in all the organs of grasses. Most intensely silicified tissues are usually root endodermis, leaf epidermis, and abaxial epidermis of inflorescence bracts Fig. (25), Kumar *et al., (*2017), Stated that, in most cases, silica impregnates the cell walls, directly laid down onto the cell wall matrix (The composition of the silicifying matrix may vary between species and cell types, thus influencing silicification pattern Guerriero *et al.,* (2016); Hodson, (2016). In particular, grasses have a unique hemicellulose composition, containing glucuronoarabinoxylan and mixed-linkage glucans, instead of the xyloglucan in non-commelinid monocots and dicots. Furthermore, grass cell walls contain more phenylpropanoid and less pectin compared with dicots Guerriero *et al.,* (2016). Silica is often proposed to crosslink the cell wall polymers, adding to their compressive strength Currie and Perry, (2009); He *et al.,* (2013); Kido *et al.,* (2015), similar to the role of lignin in lignified walls Salmén, (2015). In addition, structural tradeoff between silica, lignin and cellulose was observed in rice Suzuki *et al.,* 2012, Yamamoto *et al.,* (2012) and in a number of wetland species Schoelynck *et al.,* (2010).

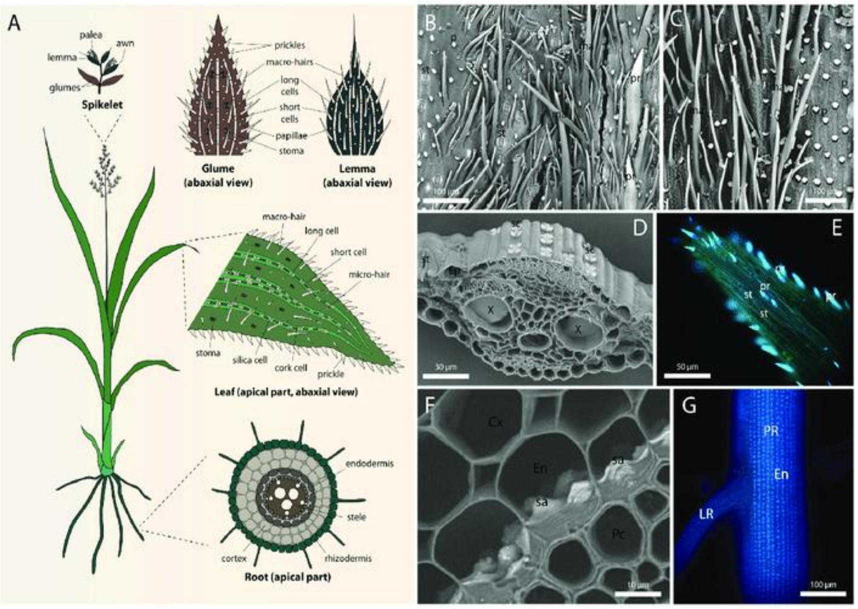

Fig. 25: Illustrates silica deposition in grasses. (A) Diagram showing a full view of a generalized grass, and typical silicification patterns in the inflorescence (top), leaf epidermis (middle), and root cross-section (bottom). White represent silicified cells. (B) Scanning electron micrograph (SEM) of the abaxial epidermis of glume in Triticum aestivum L. (C) SEM of the abaxial epidermis of lemma in T. aestivum. (D) SEM of Sorghum bicolor (L.) Moench leaf cross-section showing silica cells in the epidermis. (E) Fluorescence micrograph of prickles at the leaf tip in S. bicolor visualized by alkali-induced fluorescence Soukup *et al.,* (2014). (F) SEM of S. bicolor root cross-section showing silica aggregates anchored in the inner tangential cell walls of endodermis. (G) Alkali-induced fluorescence micrograph of S. bicolor primary root showing extensive distribution of silica aggregates in the endodermis. Root cortex was mechanically removed to expose the inner tangential cell walls. **(Cx),** cortex; **(En),** endodermis; **(Ep)**, epidermis; **(LR),** lateral root; (**ma)**, macro-hair; **(p)**, papilla; **(Pc),** pericycle**; (PR**), primary root; **(pr),** prickle cell; **(sa),** silica aggregate; **(sc),** silica cell; **(st),** stoma. SEMs were collected at the back scattered electron mode, rendering silicon atoms brighter than carbon atoms. After Kumar *et al.* (2017)

As the metabolic costs of silica deposition were estimated to be 20-fold lesser than that of lignification Raven, (1983), Fig. (26), silicification can present preferable solution for improving mechanical properties of plant tissues. However, silica seems not to provide water-repelling propertiescomparable to lignin and its utilization thus require some degree of regulation Soukup *et al.,* (2017).

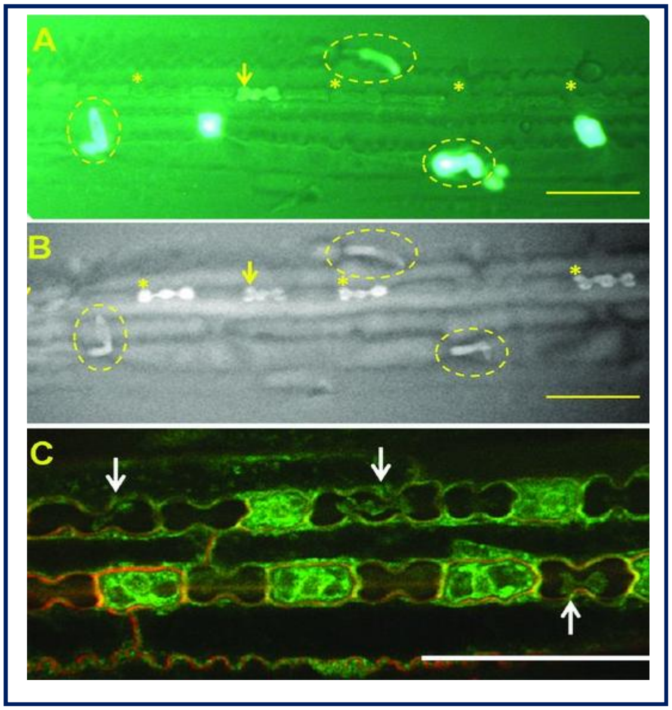

Fig. 26: Illustrates silica deposition in the epidermis of sorghum leaf. (A) Viability assay of epidermal peel showing viable cells' cytoplasm green. Viable silica cells are indicated with arrows whereas dead silica cells are indicated with asterisks. Micro-hairs are shown with broken ovals. (B) Back-scattered electron micrograph of the same field of view, showing high signal intensity emanating from viable silica cells (arrow) and micro-hairs (broken oval). Dead silica cells are already silicified (asterisks), although one dead non-silicified silica cell can also be seen [compare (A, B)]. (C) Silica cells displaying shrunken but viable cytoplasm (arrows) indicating extra-membranous silica deposition. After Kumar *et al., (*2017)

5. Role of Si in prevention of heavy metal toxicity

5.1. Silicon and Manganese Toxicity.

The role of Si in suppression of heavy metal toxicity is broadly noted in higher plants. The alleviating role of Si against Mn in the solution culture of barley was first discovered in 1957 Williams and. Vlamis (1957). Although Si is not able to affect the whole Mn in barley leaves, it is able to evenly distribute Mn across the entire leaf and does not allow Mn to concentrate in distinct necrotic spots Shi etal (2005). Additionally, the function of Si in alleviating Mn toxicity has been widely reported in rice Ma (2004) pumpkin Ma *et al.* (2001), Iwasaki and Matsumura (1999), barley Horiguchi and Morita (1987)], sorghum Galvez *et al.* (1989) maize Doncheva *et al.* (2009) beans Horst and Marschner (1978), soybeans Kluthcouski and. Nelson (1980), cucumbers Maksimovic *et al.* (2007) Shi *et al.* (2005), Shi and Zhu, (2008), and cowpeas Iwasaki *et al.* (2002) Iwasaki etal (2002), Si Horst etal (1999) can adjust the cation binding ability in the cowpea cell wall. Silicon is able to suppress Mn toxicity either by reducing the soluble apoplastic concentration of Mn in the cell wall or with apoplastic Mn detoxification Iwasaki *et al.* (2002). The results of a study by Iwasaki *et al.,*show that released Si can cause Mn oxidation in the deposited form via relation with apoplast phenolic substances, which results in improving the tolerance of leaves to Mn Iwasaki *et al.* (2002),. Silicon can decrease Mn toxicity by binding the majority of Mn in the cell walls of leaf tissues, and only a small amount of Mn is found in the symplast Rogalla and Romheld (2002). Silicon suppresses Mn toxicity in cucumbers by reducing the effects of membrane lipid peroxidation and increasing the enzymatic and nonenzymatic activities of antioxidants Shi *et al.* (2005).

5.2. Silicon and Cadmium Toxicity.

Silicon can decrease cadmium (Cd) toxicity created by increasing the pH through a detoxification process. It has been reported that Cd uptake in plants is reduced through increasing obtainable Si and raising the pH Chen *et al.* (2000). The role of Si as a supplementation factor that is effective in decreasing Cd toxicity has been reported in cucumbers Feng etal (2010), maize Vacul΄ık *et al.* (2009), da Cunha *et al.* (2008), rice Zhang *et al.* (2008), Shi *et al.* (2006), Brassica Chinensis Song *et al.* (2009), and peanuts] Shi *et al.* (2010). Silicon minimizes metal ion absorption and limits the transformation of toxic metals between the roots and shoots of rice seedlings grown in Cd Shi *et al.* (2005). Deposition of Si around the endodermis provides the potential to control Cd apoplastic transportation by physically obstructing the apoplast bypass flow in the root Shi *et al.* (2005). The Si treatment of maize under Cd stress significantly increased the biomass of the plant by reducing Cd availability and increasing soil pH Liang *et al.* (2005). The alleviating function of Si on Cd toxicity is not limited to the immobilizing role through increased pH of soil; Si also aids in Cd detoxification in maize Liang *et al.* (2005). Silicon has a similar role in increasing the tolerance of plants to Mn and Cd toxicity by immobilizing the metals in the cell walls of the root and inhibiting their transport to the cytosol Iwasaki *et al.* (2002), Iwasaki etal (2002) Rogalla and. Romheld (2002). These studies have suggested that Si is able to covalently bind with heavy metals and form an unstable silicate form Fig. (27), which subsequently suppresses the toxicity of the metals and is easily degraded to silicon dioxide (SiO_2).Hence Si displays crucial role in intercellular and extracellular parts of plants' cells. The extracellular activities of Si are by limiting penetration of heavy metals into the cytoplasm depending on its Si concentration. Sequestering of heavy metals in vacuoles is the intercellular activity of Si that happened in cytoplasm.

5.3. Silicon and Aluminium Toxicity.

The suppressive effect on aluminium (Al) toxicity in plants by Si treatment and the potential mechanisms of this suppression have been thoroughly investigated. The role of Si in the alleviation of Al toxicity is different between plant species. In this regard, Si can significantly decrease Al toxicity in Zea mays (Teosinte L. ssp. Mexicana), barley (Hordeum vulgare L.), soybeans (Glycine max L. Merr), and sorghum (Sorghum bicolor). However, in other species such as wheat (Triticum aestivum L.), rice (Oryza sativa L.), pea (Pisum sativum L.), and cotton (Gossypium hirsutum), Si is not effective in decreasing Al toxicity Hodson and Evans (1995).Additionally, using Si as an alternative detoxification method for Al toxicity has been reported in sorghum (Sorghum bicolor L.) Galvez and Clark (1991), Baylis *et al.,* (1994), tomato (Lycopersicum esculentum L.) Peaslee and Frink (1969), and barley (*Hordeum vulgare* L.) Yongchao and Ruixing (2002). It has been documented that Al toxicity containment by Si in soybeans is not stable and depends on the pH Baylis et al. (1994). The Al concentration can increase during Si treatment by forming hydroxyl-aluminosilicate complexes in the shoots of the plant. Because of the increasing concentration, the amount of Al transportation raised between the roots and shoots Birchall (1990). Moreover, Si is able to increase the Al tolerance of maize through phenolic compound metabolism, leading to more phenolics substances in the plant Kidd *et al.,* (2001). Catechin, quercetin, and other flavonoid-phenolics could potentially increase the heavy metal tolerance of plants.

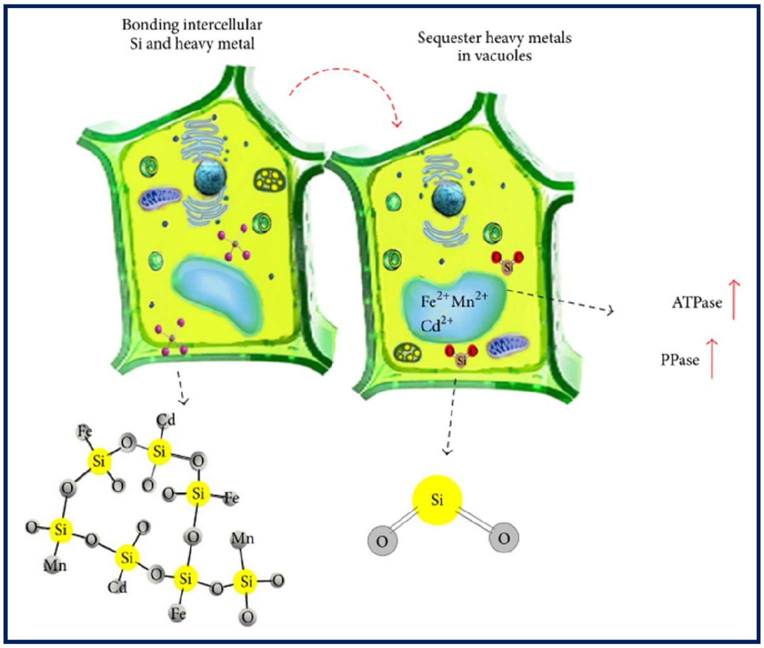

Fig. 27: Interaction between intercellular Si and heavy metals. After Mahbod etal (2015)

5.4. Silicon and Biotic Stresses

5.4.1. Silicon and Plant Disease.

Reportedly, Si is able to decrease the susceptibility of rice against sheath blight diseases Zhang *et al.,* (2006), Cai *et al.,* (2008), Rodrigues and Datnoff, (2005). Plant opal or glass and hard coating of SiO_2 polymerization in the plant cuticle layer is the possible mechanism for reducing disease susceptibility by Si Rodrigues *et al.,* (2003) Fig. (28).The physical hindrance created by SiO_2 enhances the incubation period in the leaf sheath of rice and results in impeding R. solani penetration to decrease the number and extension of sheath wounds. In comparison to the physical hindrance to early penetration, the lesion extension is a more important factor in terms of resistance to sheath blight disease, particularly in susceptible cultivars Peters *et al.* (2001).

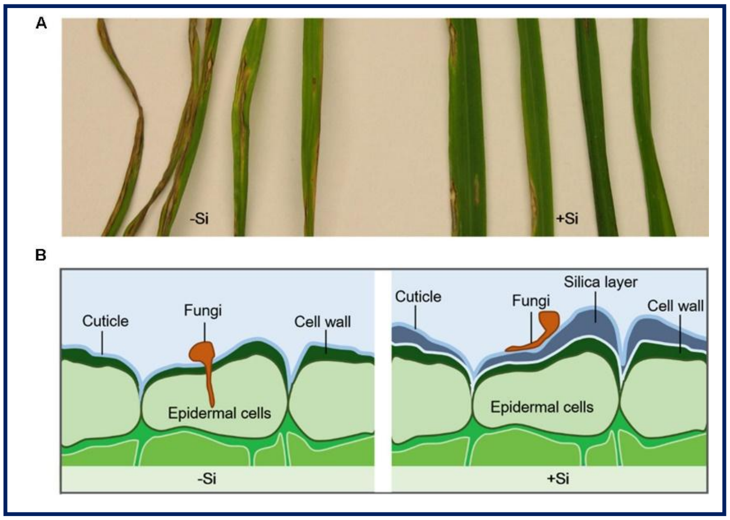

Fig. 28: Illustrates the effect of silica for enhancing plant resistance: (A) Leaf blast symptoms in rice after inoculated with Magnaporthe grisea for 10 days Sun *et al.,* (2010). Rice plants were continuously treated with (+Si) or without silicon (–Si). (B) Silica layer was formed in the cell wall of Si-treated

plants and to fungi infection by physical barriers. After Wang *et al.,* (2017), Abou seeda *et al.,* (2019), (2020)

Silicon leads to increase the sheath blight resistance through creating a physical hindrance by SiO_2 and reduce the intensity of disease. It has been speculated that Si is able to decrease the effect of sheath blight by motivating the defence mechanisms of the crops against pathogenesis, increase the amounts of phenolic components, and increase the activities of peroxidase, chitinases, polyphenoloxidase, β-1, 3-glucanases, and phenylalanine ammonialyase enzymes Rodrigues *et al.,* (2003). Several studies have reported the suppressive role of Si on rice blast disease caused by Magnaporthe grisea Cai *et al.,* (2008), Rodrigues *et al.,* (2004), and Seebold Jr, *et al.,* (2004).Silicon can reduce the intensity of blast disease in the leaf and the panicle during different growth stages. Reduction of the leaf lesions of rice after 96 hrs of inoculation with M. grisea between Si-treated and untreated plants has been examined by Rodrigues *et al.,* (2004). The experiment results indicated numerous coalescing and large lesions, regularly surrounded by a chlorotic halo, were observed on leaves of the untreated plant. However, separate and tiny lesions that seemed to be restricted at the expansion step were observed in Si-treated rice. Moreover, leaves of the control plants presented strong chlorosis compared to the Si-treated plants. Fig. (29).

Fig. 29: Illustrates rice Blast - different grades of leaf lesion. After Nettleton etal (2019)

The intensity of neck and leaf blasts in both sensitive and partially resistant rice cultivars can be decreased via Si treatment depending on the rate of Si application and the disease severity Seebold Jr *et al.,* (2000) Fig. (30).Superior inherent disease severity at specific sites needs a lot of Si fertilizer to decrease the neck and leaf blast disease as effectively as in resistant rice cultivars. The Si has been applied to prevent the occurrence of powdery mildew disease, one of the plant diseases created by Sphaerotheca fuliginea. Silicon has been reported to be an effective suppressor of powdery mildew (*Blumeria graminis*) Remus-Borel *et al.,* (2005), Liang *et al.,* (2005), Fauteux *et al.,* (2006). Increasing Si content in cucumber shoots leads to a decrease in powdery mildew incidence Miyake and Takahashi (1983). Additionally, the occurrence of powdery mildew disease decreased after increasing the concentration of Si in the culture solution Kanto (2002).The macroelements can decline infection efficiency, colony size, and conidia germination in cucumbers Menzies *et al.,* (1991). Effective use of Si in a foliar approach has been reported to help the growth of leaves in grapes, cucumbers (*Cucumis sativus*), and muskmelons (*Cucumis melo*) Bowen *et al.,* (1992), Menzies *et al.,* (1992).

Fig. 30: Illustrates Symptom of rice blast on different plant parts: **(a)** leaf blast, **(b)** Neck rot, **(c)** Collar rot, **(d)** Panicle blast. After Pusadkar Pratik Prabodhrao (2018).

The growth trend most likely depends on the Si deposition on the surface of the leaves. Silicon also increases the tolerance of cucumber roots against P. aphanidermatum and Pythium ultimum fungal diseases Cherif *et al.,* (1994). Silicon also has prohibitive effect on rice green leafhoppers (Eurymela distinct), leaf spiders, brown plant hoppers Savant *et al.,* (1996), whitebacked plant hoppers, and mites (Lorryia Formosa) Sujatha *et al.,* (1987). Along with all the above, the resistance of rice to the brown plant hopper (Nilaparvata lugens) is related to the Si content of plant Sujatha *et al.* (1987).Furthermore, it has been document that Si is able to increase the tolerance of sorghum (Sorghum bicolor) to anthracnose Resende *et al.* (2013).

5.4.2 Membrane proteins involved in silicon uptake

Ma *et al.,* (2006,2007) have identified for the first time two genes involved in Si uptake and translocation in plants, one of which is an aquaporin (Lsi1) mediating the passive entry of silicic acid with water. In contrast, the other is a type of cation transporter with efflux activity (Lsi2) Fig. (31).

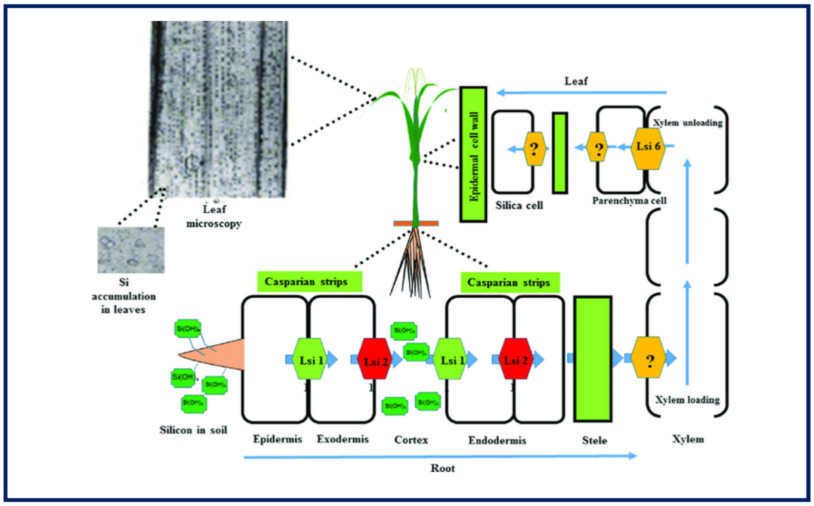

Fig. 31: Illustrates a schematic representation of Si uptake, transport, and accumulation in rice. Silicic acid from the soil solution is absorbed by the roots, transported to the root exodermis by the influx transporter (Lsi1), and subsequently released to the apoplast by the efflux transporter (Lsi2). Subsequently, it enters the root endodermis via Lsi1 is released to the stele portion of the root via Lsi2.

Finally, silicic acid is translocated by an unknown transporter into the xylem and transported to the shoots via the transpiration stream. In the leaves, silicic acid is unloaded by another influx transporter (Lsi6) and localized in the xylem parenchyma cells of leaf sheaths and leaf blades. In the shoots and leaves, Si is transformed from an aqueous form (silicic acid) to solid amorphous silica (SiO2-nH2O) and primarily deposited in the cell walls of different tissues, such as leaf epidermal cells. After Yan *et al., (*2018).

Khan *et al.,* (2019) stated that after absorption by the roots, Si is transported to other parts of the plant via the xylem of the roots Ma and Yamaji (2008). With the loss of water from a plant, inorganic amorphous oxides of silicic acid crystalize and precipitate, forming solid silica bodies called opal phytoliths that accumulate in the extracellular or intracellular spaces of plants, e.g. in the cell wall and trichomes Ma *et al.,* (2006); Cooke and Leishman, (2011). However, the mechanisms that prevent silicic acid polymerizing in the cell wall are not clear. Recently, it has been reported that the low silicon (Lsi1, Lsi2, and Lsi6) genes are responsible for Si uptake in the roots and its distribution to other organs in barley, rice, and cucumber, and maize Wang *et al.,* (2015b). The Lsi2 gene is expressed in the root endodermis and is considered a putative anion transporter Ma *et al.,* (2007), Mitani *et al.,* (2011). On the other hand, the Lsi1 and Lsi6 transporters belong to the aquaporin family, have a major role in Si distribution in shoot, and root tissue Mitani *et al.,* (2011). Furthermore, proton-driven transport activity has been reported in the Lsi2 transporter Ma *et al.,* (2007), and it works as a Si/H+ antiport. The leaf epidermis and cell walls accumulate 90% of the total absorbed Si, which accounts for 10% of the dry weight of grass shoots Yoshida, (1965), Ma and Takahashi, (2002); Raven, (2003).Silica that has accumulated intracellularly in the cytoplasm and vacuoles is stable even after plant decomposition and is abundant in soils Lins *et al.,* (2002). A schematic model of the Si transport system in rice Fig. (32). Action of two membrane proteins is responsible for high accumulation of Si in rice. Being a first entry point, the influx channel (Lsi1) has been extensively studied in different plant species Chiba, etal (2009); Deshmukh *et al.,* (2013); Grégoire *et al.,* (2012); Guerriero *et al.,* (2019); Sun *et al.,* (2017). Lsi1 belongs to the NIPs subfamily of aquaporins and is a Si influx channel Ma *et al.,* (2006); Sasaki *et al.,* (2016). In barley, the role of HvLsi1 in silicic acid influx has been well-characterized Chiba *et al.,* (2009). Similarly, three other Lsi1 homologues, such as ZmNIP2-1, ZmNIP2-2, and ZmNIP2-3 were found in maize Zangi and Filella, (2012). An extensive comparative genomics study performed on 25 plant genomes and 25 plant transcriptome data have shown a correlation between the absence of Lsi1 homologue and the inability of plant species to accumulate Si (>0.5% d.w.) Deshmukh, *et al.,* (2015). In contrast to Lsi1, the Si transporter Lsi2, a member of the anion transporter protein family is an energy-dependent efflux transporter Ma *et al.,* (2007). Both Lsi1 and Lsi2 are chiefly expressed in the mature region of roots, except root hairs Ma *et al.,* (2007); Sasaki *et al.,* (2016); Yamaji and Ma, (2007), (2011). In rice, Si supplementation down regulates the expression of both Lsi1 and Lsi2 genes. The corresponding proteins are located on both root exodermis and endodermis; however, with the distinct polarity, that is, Lsi1 is present on the distal side, whereas Lsi2 is located on the proximal side Fig. (32). Hildebrand *et al.,* (1997), Zangi and Filella, (2012), reported that marine diatoms can uptake Si-by-Si transporters viz. SITs through an active process utilization of Si by algae for the formation of their cell wall. Mechanism of silicon uptake is found to be active, and necessitates sodium ions. However, SIT shows no similitude to Lsi2, although they are both energy-dependent Si transporters Zangi and Filella, (2012). The uptake of Si can be impaired via knockout of Lsi1 or Lsi2, as reported in rice Yamaji *et al.,* (2012).

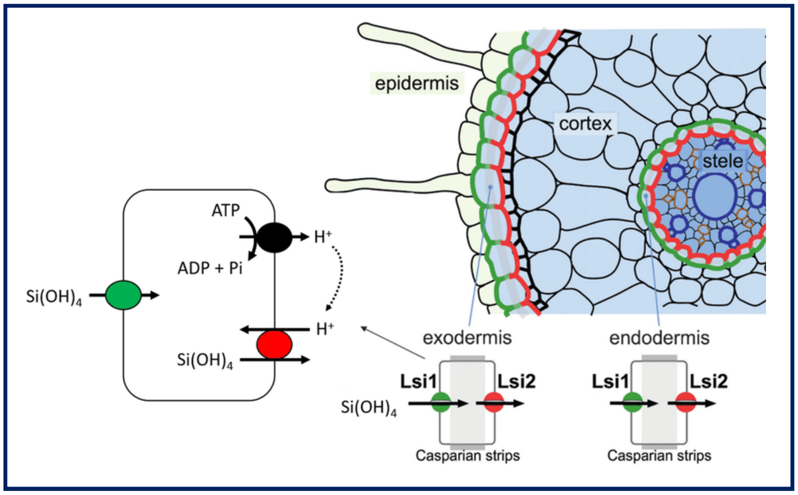

Fig. 32: Illustrates standing Si-transport model in the roots of rice (Oryza sativa). Lsi1 and Lsi2 are expressed in the distal and proximal ends, respectively, of the exodermis and endodermis. Lsi1 mediates the thermodynamically passive uniport of Si $(OH)_4$, whereas Lsi2 is thought to mediate the secondary active transport of Si $(OH)_4$ in antiport with H^+ (the electrochemical gradient of which is generated by the plasma membrane H^+-ATPase. After Ma and Yamaji (2008)

In rice, a co-operative mechanism mediated by Lsi1 and Lsi2 is responsible for the uptake of Si from soil to the roots, and that explains the high amount of Si found in this monocot. Several membrane proteins supposed to be responsible for Si uptake and be noted that members of the Lsi1 family have been modelled in silicoGuerriero *et al.,* (2019), Ouellette *et al.,* (2017).

6. Uptake and transport of Arsenic

Arsenic (As) enters the environment via natural or anthropogenic sources and plant systems mainly absorb inorganic form of As, that is, arsenite (As (III)) and arsenate As(V) Abbas *et al.,* (2018); Dutta & Bandopadhyay, (2016) Fig. (33).

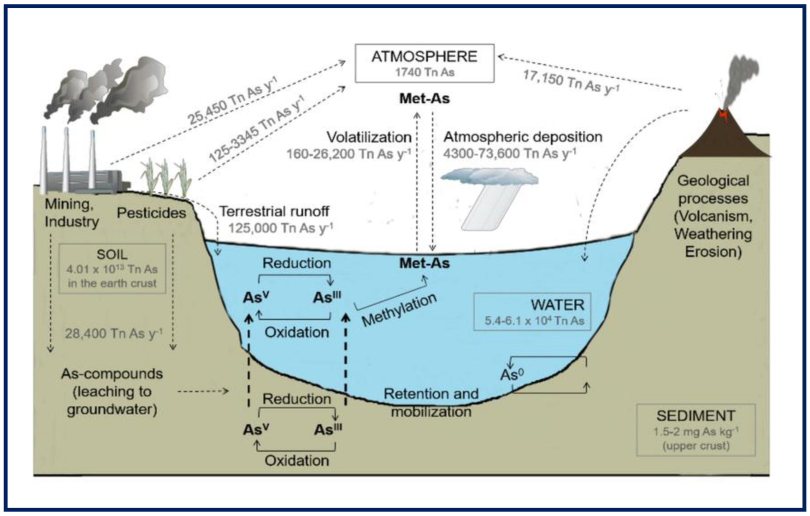

Fig. 33: Illustrates a global arsenic (As) biogeocycle afterSultana etal (2015), after Mukhopadhyay etal (2002)] with some estimated arsenic fluxes after Matschullat (2000). Met-As= methylarsenicals; As V = arsenate; As III = arsenite; As 0 = arsenic; t = tons; t y −1 = tons per year. After Laura Barral-Fraga *et al.* (2020)

Laura Barral-Fraga *et al.* (2020) arsenic enters the atmosphere through dust particles coming from volcanic emissions (ashes), wind erosion, low-temperature volatilization from soils, marine aerosols, and pollution and is returned to the Earth's surface (mainly to water bodies) by atmospheric deposition; then, it moves through terrestrial runoff and groundwater discharge to the water bodies Fig.(33). There, it binds to or (co)precipitates with suspended particles and tends to sink to the sediments Mukhopadhyay *et al.* (2002), Sultana *et al.* (2015). Arsenic is a constituent of more than 200 minerals Garelick *et al.* (2009), and is primarily present in chemically reduced forms, like realgar (AsS), orpiment (As_2S_3), and arsenopyrite (FeAsS), the latter being the most abundant arsenic ore Smedley and Kinniburgh (2002). Natural geological sources are some of the most significant causes of arsenic contaminated groundwaters around the world Safiuddin (2011), Alonso *et al.* (2014). Arsenic contamination is frequently observed in soils, sediments, and water. While baseline arsenic concentration is on average below 1 μg L^{-1} , values above 10 μg L^{-1} are commonly reported in polluted European rivers Smedley and Kinniburgh (2016), Smedley and Kinniburgh (2002). High arsenic concentrations in surface waters is in most cases attributed to the discharge of groundwaters (in cases with values up to 21,800 μg As L^{-1}), mining activities (values can reach 7900 μg As L^{-1}), or the influence of geothermal activity (values up to 370 μg As L^{-1}), as reviewed by Smedley and Kinniburgh (2002) Smedley and Kinniburgh (2016) . Arsenic can be mobilized in gold mining extractions, due to its co-occurrence with gold Garelick *et al.* (2009), and through other arsenic anthropogenic inputs, including indiscriminate use of certain pesticides and herbicides, as well as of wood preserving arsenicals Garelick *et al.,* (2009), Azizur Rahman and Hasegawa (2012)

Ma *et al.,* (2001) stated that terrestrial plants have lower ability to uptake As from soils in comparison to wetland plants, and this phenomenonis reported in Pteris vittata. For the entrance into root symplast, As crosses the plasma membrane of the root endodermal cells, possibly by the action of a membrane pump or it can enter into the root via the apoplastic pathway Dutta and Bandopadhyay, (2016).Arsenite is actively transported inside the plant cells by nodulin 26-like intrinsicproteins (NIPs), usually referred to as aquaporins Bienert *et al.,* (2008); Deshmukh *et al.,* (2017); Dutta and Bandopadhyay, (2016). NIPs are implied in bidirectional movement, allowing the influx as well as the efflux of As (III) (Pommerrenig *et al.* (2015). However, in contrast to arsenite, the influx of arsenate in plants occurs through phosphate transporters viz. Pht1;1 and Pht1;4 Shin *et al.,* (2004); Xu *et al.,* (2015). The mechanisms that regulate the influx of monomethyl arsenic acid (MMA) and dimethylarsinic acid (DMA), that is, the organic arsenicals, are still unclear Dutta and Bandopadhyay, (2016); Zhao *et al.,* , (2009) Fig. (34). Moreover, the overall process that operates the As acid transfer from the roots to the shoots after theabsorption has hardly been studied in diverse plant species Farooq *et al.,* (2016). Different plant species show varying tendencies to accumulate and tolerate As concentrations; for example, some ferns such as P. vittata and P. cretica are considered as As hyperaccumulators because they can efficiently translocate As from the roots to frondsDutta & Bandopadhyay, (2016); Wang *et al.,* (2002).

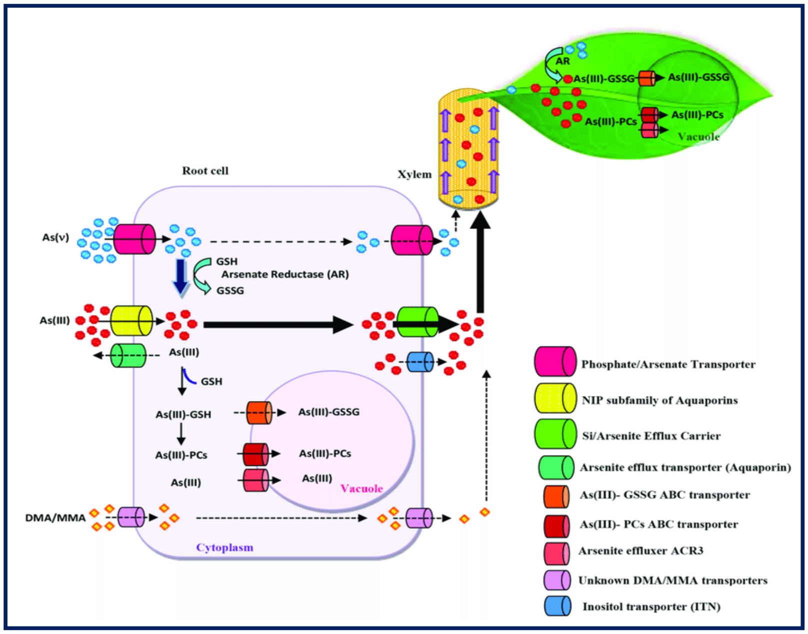

Fig. 34: Illustrates a overview of Arsenic (As) uptake, transport, translocation, and detoxification in plants. Arsenate (AsV) uptake can occur via phosphate transporters. AsV reduction occurs in root cells before xylem loading and transportation to shoots. Arsenate reductase (AR) reduces AsV to arsenite (AsIII) by using glutathione (GSH) as a reductant. AsIII uptake occurs via nodulin 26-like intrinsic (NIP) aquaglyceroporin channels. Arsenic methylated species (DMA/MMA) uptake is carried out by unknown transporters or by NIP. Phytochelatins (PCs) and GSH coordinate with AsIII to form a variety of complexes that are sequestered in vacuoles by ABC-type transporters. In Pteris vitatta, As(III) can also be transported to the vacuole by Arsenical Compound Resistance3 (ACR3) effluxer. As loading to the xylem can be mediated by the Si/Arsenite efflux transporters or inositol transporters (INT). The considerable capacity for As root-to-shoot translocation and vacuolar sequestration in shoots ensures high As deposition levels in the above-ground part. After Souri *et al.* (2017)

6.1. Arsenic transporter

The transport of arsenate occurs via the phosphate transporters Shin *et al.,* (2004), Tripathi *et al.,* (2007). In Arabidopsis thaliana, AtPht1;1 (Pi transporter 1;1) and AtPht1;4, transporters assist in the acquisition of inorganic phosphorus and arsenate at higher as well as lower phosphorus level Farooq, *et al.,* (2016); Shin *et al.,* (2004). Furthermore, OsPht1;1 localized in plasma membrane is known to have higher affinity for the Pi uptake, and it also showed involvement in the uptake of As(V) Farooq *et al.,* (2016); Jia *et al.,* (2011); Kamiya *et al.,* , (2013); Sun *et al.,* (2012); Wu *et al.,* (2011). Moreover, AtPht1;1 and AtPht1;7 are known to be oversensitive to arsenate but insensitive to As(III), and as reported in Arabidopsis LeBlanc *et al.,* (2013). In rice, arsenite is uptaken by the same system shown to mediate Si uptake, Lsi1 and Lsi2, and then translocated likewise, because arsenite and silicic acid possess similar chemical properties Ma *et al.,* (2008); Song *et al.,* (2014). However, some other transporters were reported to transport As (III) Bienert *et al.,* (2008); Ma *et al.,* (2008); Mitani-Ueno *et al.,* (2011); Song *et al.,* (2014). The contribution of few WRKY transcription factors is recognized in the influx of As (V) Fig. (35).

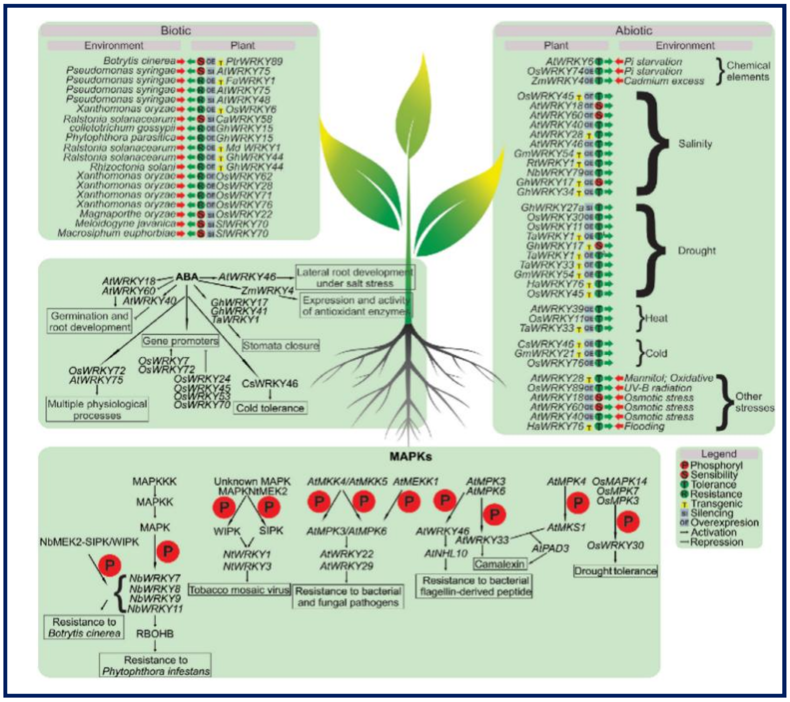

Fig. 35: Illustrates a overview of the most recent reports concerning WRKY roles in plant defense, including the relationships with MAPKs, ABA signaling, and responses to biotic and abiotic stresses. After Finatto, *et al., (*2018)

Finatto *et al.,* (2018) stated that WRKY transcription factors (TFs) are responsible for the regulation of genes responsive to many plant growth and developmental cues, as well as to biotic and abiotic stresses. The modulation of gene expression by WRKY proteins primarily occurs by DNA binding at specific cis-regulatory elements, the W-box elements, which are short sequences located in the promoter region of certain genes. In addition, their action can occur through interaction with other TFs and the cellular transcription machinery. The current genome sequences available reveal a relatively large number of WRKY genes, reaching hundreds of copies. Recently, functional genomics studies in model plants have enabled the identification of function and mechanism of action of several WRKY TFs in plants. This review addresses the more recent studies in plants regarding the function of WRKY TFs in both model and crop plants for coping with environmental challenges, including a wide variety of abiotic and biotic stresses

In plants, As (V) defence is facilitated by WRKY6 and WRKY45 (the WRKY transcription factors), and they also regulate AtPht1;1 expression and alter As (V) uptake in plants Castrillo *et al.,* (2013); Farooq *et al.,* (2016); Wang *et al.,* (2007), and As(V) can suppress the activation of those genes which participate in Pi starvation, and this was reported in a study on P. vitatta by DiTusa *et al., (*2016). During this study, they characterised and recognized three Pht1 transporters, and also revealed that PvPht 1;3 and AtPht1;5 have identical affinities for phosphate, whereas the affinity of PvPht1;3 for arsenate is relatively higher in comparison to phosphate Farooq *et al.,* (2016). Plant aquaporins also take part in As(III) entry Farooq *et al.,* (2016); Kamiya *et al.,* (2009); Mukhopadhyay *et al.,* (2014). Several NIPs such as OsNIP2;1, OsNIP2;2 and OsNIP3;2 reported in rice, AtNIP5;1, AtNIP6;1 and AtNIP7;1 reported in A. thaliana, LjNIP5;1, LjNIP6;1 reported in Lotus japonicus enhanced As(III) sensitivity in yeast Bienert *et al.,* (2008); Pommerrenig *et al.,* (2015). Katsuhara *et al., (*2014) described that few NIPs viz. OsNIP 3;3 and HvNIP1;2 are also permeable to As(III). Recently, Xu *et al., (*2015) provided information that AtNIP3;1 present on Arabidopsis roots can transport As(III). Apart from NIPs, a few plasma membrane intrinsic proteins (PIPs), for instance OsPIP 2;4, OsPIP 2;6, and OsPIP 2;7 are also involved in the As(III) uptake and tolerance in rice Farooq *et al.,* (2016); Mosa *et al.,* (2012). In Arabidopsis tissues, the role of OsPIP2;4, OsPIP2;6 and OsPIP 2;7 in tolerance against high As(III) stress was validated by their overexpression. In yeast cells, PvTIP 4;1, an aquaporin, assisted As(III) diffusion, whereas in transgenic Arabidopsis, its overexpression enhanced As accumulation and susceptibility. The involvement of PvTIP 4;1, a new tonoplast intrinsic proteins (TIPs), in the influx of As(III) in P. vittata was noticed Farooq *et al.,* (2016); He *et al.,* (2016). Currently, Duan *et al., (*2015) have put forward that to load As (III) into the phloem; plants utilize sugar alcohol, inositol transporter.

7. Uptake and transport of antimony

Feng *et al.,* (2013) Shtangeeva *et al.,* (2011); Tschan *et al.,* (2008), reported that mechanism of both Sb (V) and antimony (Sb) uptake show identical behaviour because of their similar electronic structure, their uptake route is different from each other. According to Asher and Reay (1979), arsenate uptake occurs through the phosphate pathway; however, some pieces of evidence suggest the P (V) pathway does not mediate that Sb uptake. Tschan *et al., (*2008) observed that in Zea mays or Helianthus annuus phosphate application did not decrease Sb (V) uptake; thus, it was inferred that the influx of Sb (V) could not take place via the phosphate uptake system. If the uptake of Sb(V) does not occur through the phosphate path, then the question that needs to be addressed is which route or mechanism is allowed for the entry of Sb(V) into the plant Feng *et al.,* (2013). Tschan *et al.,* (2009) reported that two hypotheses that are related to Sb(V) uptake were **(a)** the entry of Antimonite in root symplast occurs via anion transporters like those that transport (Cl^-) or (NO_3^-) with low selectivity, and **(b)**Antimonite enters the xylem via the apoplastic route by crossing either partially sealed or damaged Casparian strip. In the case of plants, the second mechanism is considered to be more appropriate by some authors Feng *et al.,* (2013), Feng *et al.,* (2013). Meharg and Jardine (2003), reported that there is acompetition between Sb (III) and As (III), in rice experiment indicating that Sb(III) and As(III) may utilize similar uptake pathways. The reason behind this is that As(III) uptake was recognised to be facilitated by aquaporins and that the uptake of Sb(III) in plants also takes place in a passive manner through aquaporins similar to what was observed in yeast (Saccharomyces cerevisiae) Wysocki, *et al., (* 2001) and rice Meharg and Jardine, (2003). Ars B and Ars A, which generally consists of two nucleotide-binding sites, accelerate the export of Sb (III) in Escherichia coli. However, in the case of As or Sb, it has only one binding site. When ArsA binds to metalloids, then its ATPase activity is triggered, and the metalloid binding site in ArsA shows its involvement in the translocation of As (III) or Sb (III) across the membrane via ArsB Zhou, *et al.,* (2000). The Acr3 is located in the yeast plasma membrane and it is known to facilitate the export of As (III) and Sb (III) and thus imparting to confer resistance to As (III) and Sb (III) Tamás (2016).

Antimony first needs to cross the plasma membrane before entering the cell Tamás, (2016). After the uptake by the roots, it is transported to the shoot from where it flows to the leaves and ultimately reaches the fruits Koreňovská, (2006); Pierart *et al.* (2015); Shtangeeva *et al.* (2012). Furthermore, Sb is found in every plant tissue. Feng *et al., (*2013) observed that the phyto-availability of Sb depends on many factors such as its solubility, as well as its capacity to be transferred from thesolid-state to the soil solution. However, in soils, the solubility of Sb is very low, although it depends mainly on the soil characteristics Pierart *et al.,* (2015). Metalloids accumulate in different plant sites in high amount often found in edible parts Pierart *et al.,* (2015). P. vitatta, an As hyperaccumulator, is sometimes also known as Sb hyperaccumulator. For example, when it is grown in the presence of high concentrations of Sb, four types of Sb, like Sb (III), Sb (V), $Sb(CH_3)_3$, have been found Müller *et al.,* (2015) Fig.(36).

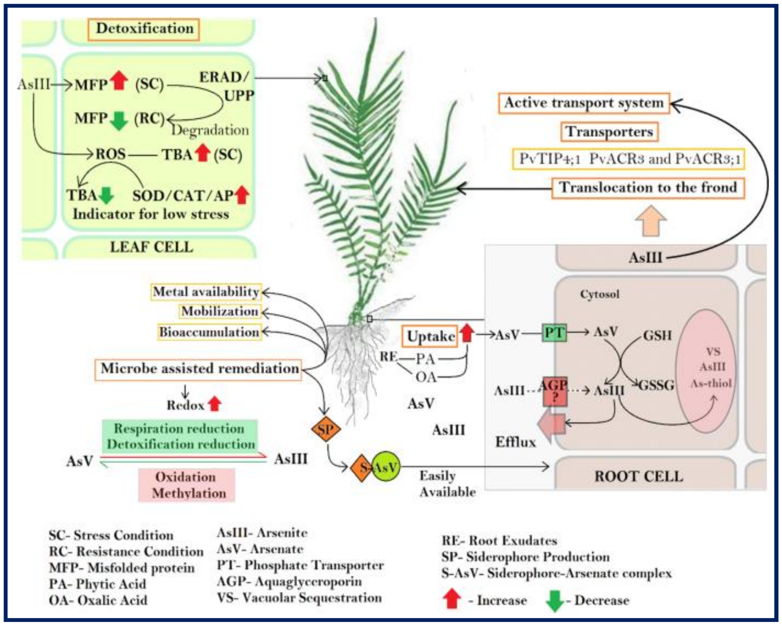

Fig. 36: Illustrates mechanism of As-uptake and transport in *P. vittata*, for its potential use in phytoremediation. After Vandana *et al.* (2020)

Recent findings have demonstrated that, like most of the metalloids, Sb(III) enters cells via aquaporin channels Biener *et al.,* (2008); Mukhopadhyay *et al.,* (2014); Rosen and Tamás (2010); Tamás (2016). The report from the laboratory of Barry Rosen revealed the aquaporin mediated transport of Sb (III). Rosen and Tamás (2010) isolated a Sb (III) resistant E. coli by using an arbitrary transposon mutagenesis approach and they mapped the transposon insertion in the glpF gene, which codes for a protein known to be involved in glycerol uptake. This genetic data revealed that GlpF may serve as an influx pathway for Sb (III) into E. coli Sanders *et al.,* (1997); Tamás, (2016) It was later revealed that the aquaglyceroporin Fps1 assists in Sb (III), as well as As (III) uptake in yeast Tamás (2016); Wysocki *et al.,* (2001), and it was the first evidence that confirmed metalloid entry in a eukaryotic organism. It was put forward by most of the reports that antimonous acid $Sb(OH)_3$is transported by NIPs and few other aquaglyceroporins Mukhopadhyay *et al.,* (2014); Pommerrenig *et al.,* (2015). The reason behind this is that antimonous acid shows resemblance to arsenous acid in its physicochemical characteristics, such as molecular volume, pKa values, electrostatic charge distribution, tetrahedral structure, ability to form hydrogen bonds, etc. and meets all of the physicochemical prerequisites to be translocated along an aquaporin route; however, MIPs Pommerrenig *et al.,* (2015), transport arsenous acid. By using heterologous expression in yeast, it was revealed that the transport of Sb(III) across the plasma membrane is mediated by NIP5;1,NIP6;1 from A. thaliana and L. japonicus, and by NIP2;1 and NIP3;2 from Oryza sativa Bienert *et al.,* (2008); Tamás, (2016). In conclusion, the above-mentioned findings revealed that aquaporins provide a molecular pathway for Sb entry in plants Tamás, 2016) Fig. (37).

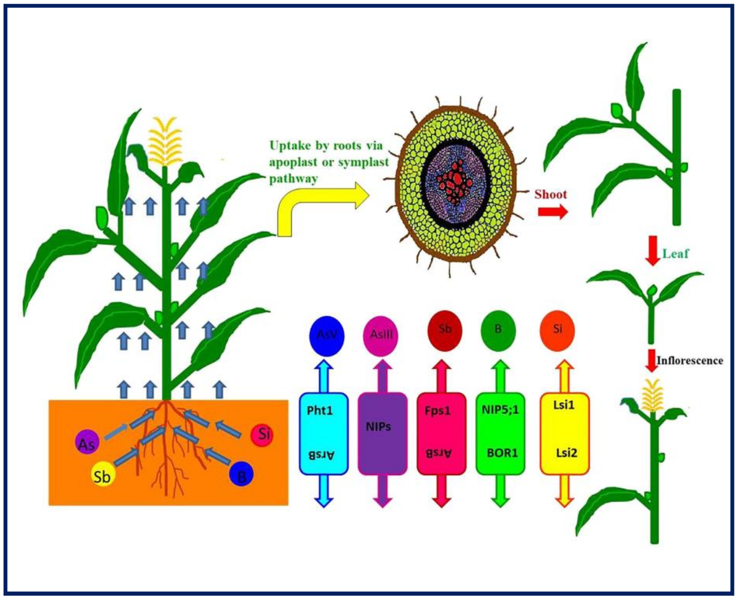

Fig. 37: Illustrates the uptake and transport of different metalloids, their influx and efflux by means of their respective transporters/channels. After Parveen *et al.* (2020)

8. Beneficial role of metalloids in plants.

As and Sb are known for their toxicity in plants, whereas Si and B fulfil useful or essential functions in plants Pommerrenig *et al.,* (2015). However, the beneficial nature of metalloids is not determined exclusively by their organic or inorganic form Alvarez et al. (2014); Kroukamp *et al.,* (2016); Stanislawska *et al.,* (2013), nor by the oxidative species present Kroukamp *et al.,* (2016); Machado *et al.,* (2006); Stanislawska *et al.,* (2013). Boron (B) takes part in the elongation of the cell, membrane and cell wall integrity, and secondary metabolism; additionally, and also involved in carbohydrate and energy metabolism, as well as the synthesis of nucleic acids Fig.(38), Blevins and Lukaszewski, (1998); Cakmak and Römheld, (1997); Camacho-Cristóbal *et al.,* (2008); Camacho-Cristóbal, etal (2011); Han *et al.,* (2009); Huang *et al.,* (2014); Redondo Nieto *et al.,* (2012); Wimmer, *et al.,* (2009). Moreover, B is involved in cell wall structure and function, metabolic activities, and it is required in improving crop yield and quality Brown *et al.,* (2002); Zangi and Filella, (2012).

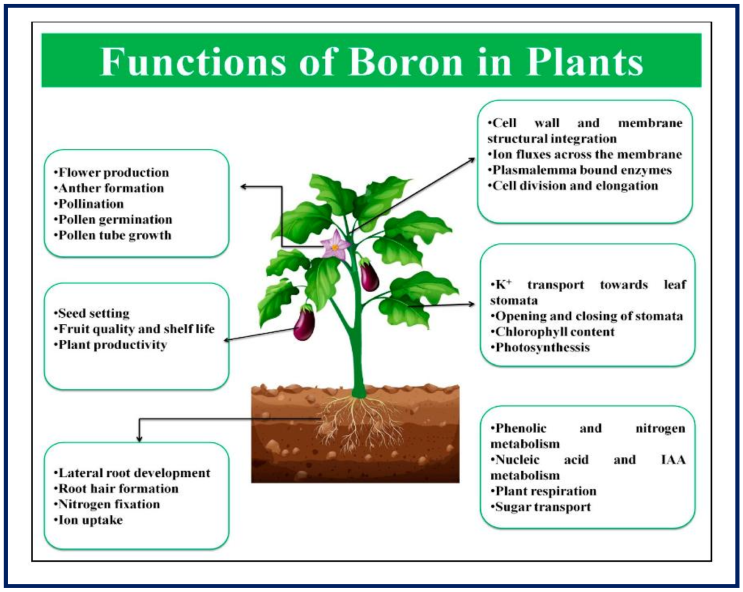

Fig. 38: Functions of B in different parts of plant. IAA: Indoleacetic acid.

It is capable of making diester bridges between cis-hydroxyl consisting of molecules and thus possesses the property of molecular linker Bolaños *et al.,* (2004), Zangi and Filella (2012). Although research studies demonstrated the nutritional vitality of B in animals, as well as humans, it is now considered as "probably vital" Zangi and Filella, (2012). Ismail and Volker (1997) suggest that B protects the plasma membrane against peroxidase damage and maintains the structural integrity. B is found to take part in cell formation and development, lignin synthesis, photosynthesis, nitrogen fixation Jahangir *et al.,* (2017); Lewis, 1980); Parr and Loughman (1983), and metabolism, as well as linked with the uptake of calcium Jahangir *et al.,* (2017). A nutrient solution containing B is advantageous for the germination and growth Davis *et al.,* (2002). Moreover, it is possibly required for the biosynthesis, as well as the transport of carbohydrates, the metabolism of nucleic acid, and the interaction with plant growth regulators Davis *et al.,* (2002), Frick, (1985). B is also very effective in overcoming plant stresses due to different abiotic factors Carvalho, *et al.,* (2020); Naeem *et al.,* (2018); Neves *et al.,* (2019), Waraich *et al.* (2012) .

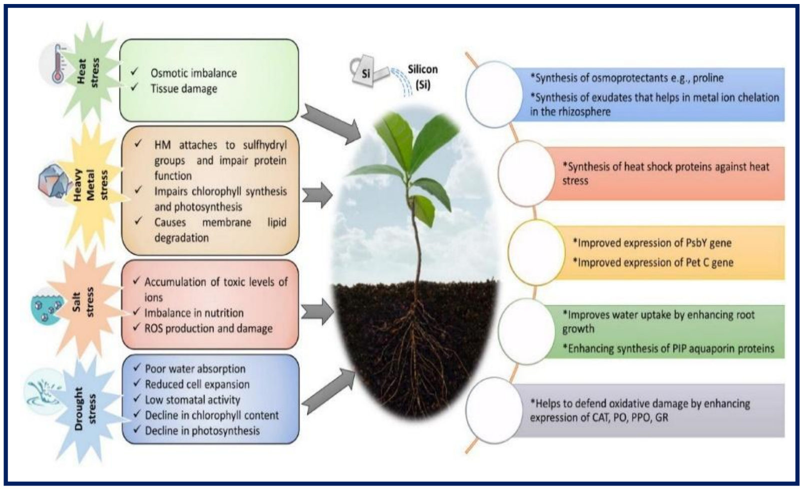

Fig. 39: Illustrates impact of abiotic stress on various aspects of plant growth and defense mechanisms evoked by application of Si. After Mir *et al., (*2022)

Si is known to enhance the resistance of plants against abiotic and biotic stresses Arif *et al.,* (2019); Epstein, (1994), Richmond and Sussman (2003); Tripathi, *et al.,* (2020); Tripathi *et al.,* (2020); Vaculík *et al.,* (2020); Vishwakarma, *et al.,* (2020); Zangi and Filella (2012). Si was revealed to increase suberization and lignification in the roots of rice Fleck *et al.,* (2010), Keller *et al.,* (2015), Fig. (39), (40) and (41). Studies have convincingly demonstrated the positive effects of Si on plant growth, especially under abiotic or biotic stresses Epstein (1999), Guntzer *et al.,* (2012); Jia-Wenet, al., (2013); Keller *et al.,* (2015); Ma and Yamaji (2006). Gunes *et al.,* (2007), showed that Si enhances stress tolerance, as well as decreases membrane damage in tomato and spinach. A study on wheat (Triticum aestivum L.) plants showed that Si application could sustain water level and dry materials content much better under drought stress compared to non-silicon treated plants Gong *et al.,* (2003). Hattori *et al., (*2005) suggested that Si treatment improved drought tolerance in Sorghum bicolor plants via increasing its water uptake capability. However, Si increases resistance to sheath blight and blight disease in rice Nakata *et al.,* (2008); Rodrigues *et al.,* (2003); Sahebi *et al.,* (2015); Zhang *et al.,* (2006).

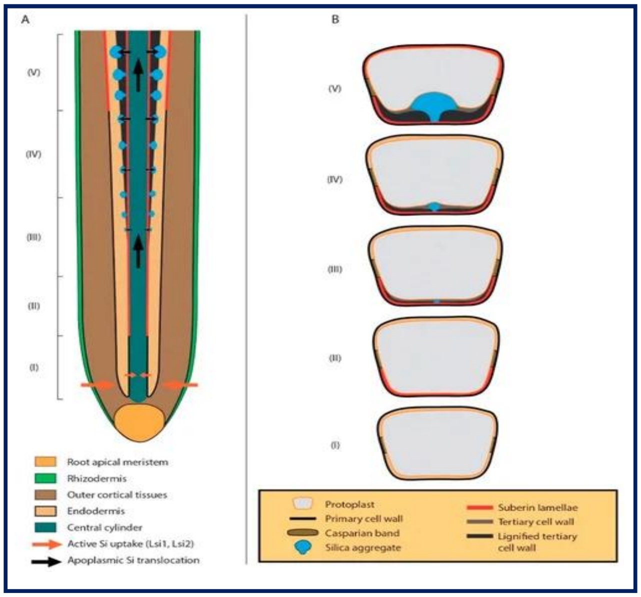

Fig. 40: Illustrates silica deposition in root endodermis of Sorghum bicolor, Soukup etal (2017), Lux, and Rost, (2012) modified; from Annals of Botany journal. (A) A longitudinal section of root showing transport and deposition of silica in endodermal cells. (B) A scheme of silica deposition in a single endodermal cell. I—Endodermal cell with primary cell wall and Casparian strip. II—Suberin lamellae deposition at the inner tangential cell wall. III–IV—Simultaneous deposition of tertiary inner tangential cell wall and the growth of a silica aggregate. Tertiary cell wall grows centripetally as an extending matrix of cellulosic and non-cellulosic polysaccharides that is progressively impregnated by the deposition of various polyphenolic substances polymerizing into lignin. The growth of silica phytoliths initiates in a spot predetermined probably by a patchy pattern of lignin polymerization or a local difference in the composition of its constituents. IV—Development of the tertiary cell wall continues and promotes further growth of the silica phytoliths. V—the growth of silica phytoliths arrests with the end of tertiary cell wall development. After Lux *et al.* (2020).

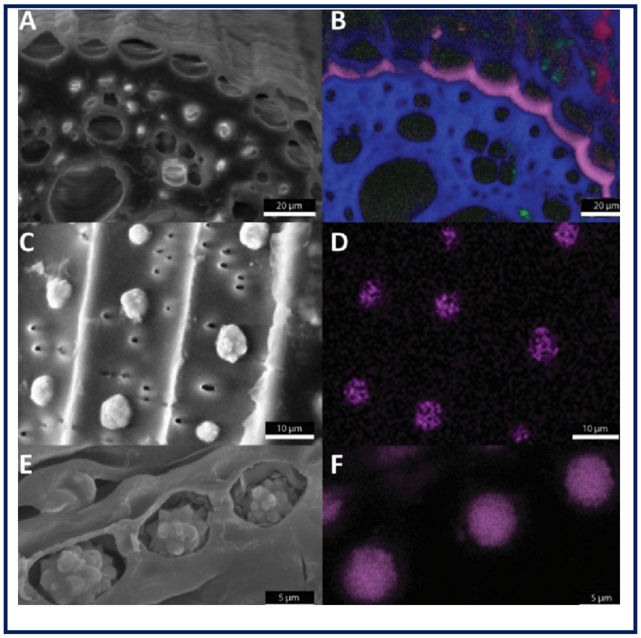

Fig. 41: Illustrates three modes of silicification in roots investigated by scanning electron microscopy (A,C,E) coupled with X-ray microanalysis (B,D,F), where Si is visualized by pink color. Impregnation of endodermal cell walls is typical for wheat (Triticum) (A, B). Silica aggregates/phytoliths associated with inner tangential cell walls of endodermis are shown in Sorghum bicolor (C, D). Specific stegmata cells filled with silica aggregates/phytoliths occur in *Phoenix dactylifera* (E, F). After Lux *et al., (*2020)

Si is known to reduce the toxic effects of high concentrations of metals in a variety of plants, for example, aluminium in T. aestivum Cocker *et al.,* (1998), cadmiumin T. saestivum Rizwan *et al.,* (2012), manganese in Cucumis sativus Rogalla and Römheld (2002), cadmium in C. sativus Feng *et al.,* (2010), cadmium in Zea mays Patrícia, *et al.,* (2008) Vaculík *et al.,* (2012) , Vaculík, etal (2009),manganese in Z. mays Doncheva *et al.,* (2009), zinc in riceSong *et al.,* (2011), cadmium in rice Nwugo and Huerta, (2008); Shi, *et al., (*2005), zinc in Cardaminopsis halleri Neumann and Zur Nieden (2001) and, cadmium in Fragaria ananassa Treder and Cieslinski, (2005). Si accumulated in tissues possibly acts as a physical barrier, and it increases the mechanical strength and rigidity of plant tissues Farooq *et al.,* 2013; Ma and Yamaji (2006). Soluble Si stimulates the defence mechanisms and enhances plant disease resistance in plants Farooq *et al.,* (2013); Fauteux *et al., (*2005). Plant resilience was enhanced significantly with the increased Si uptake in plants.

9. Plant detoxification mechanisms for metalloids

Júnior *et al.,* (2014) stated that toxicity affect plant growth and development. The agency for toxic substances and disease registry recognised metals and metalloids as toxic elements. Anjum *et al.,* (2014), Singh *et al.,* (2011), reported that after the ingestion of plants or products containing metalloids, human and animal health is impacted through the food chain The harmful impact of toxic metalloids on plant growth, metabolism, development, and even on the overall productivity has been documented by research studies Anjum, *et al.,* (2014); Candan and Tarhan (2003); Cuypers *et al.,* (2013); Gill and Tuteja, (2010); Maksymiec (2007), Schröder *et al.,* (2009); Sytar *et al.,* (2013). Metalloids can affect the productivity of plants, and the production of ROS is enhanced through different reactions Anjum, *et al.,* (2014); Candan and Tarhan (2003); Cuypers *et al.,* (2013); Gill and Tuteja, (2010); Maksymiec (2007); Schröder *et al.,* (2009); Sytar *et al.,* (2013).Anjum *et al.,* (2014); Berni *et al.,* (2019); Mullineaux and Karpinski, (2002); Scandalios (2002), noticed that in several studies that ROS are signalling molecules which take part in many of the physiological progression like in cell division cycle, apoptosis, regulation of the gene, stress perception, hypersensitive reaction, as well as in senescence ROS are also able to trigger and /or induce plants' responses to a range of environmental stimuli Anjum *et al.,* (2014), Mullineaux and Karpinski, (2002); Scandalios, (2002), Fig. (42).

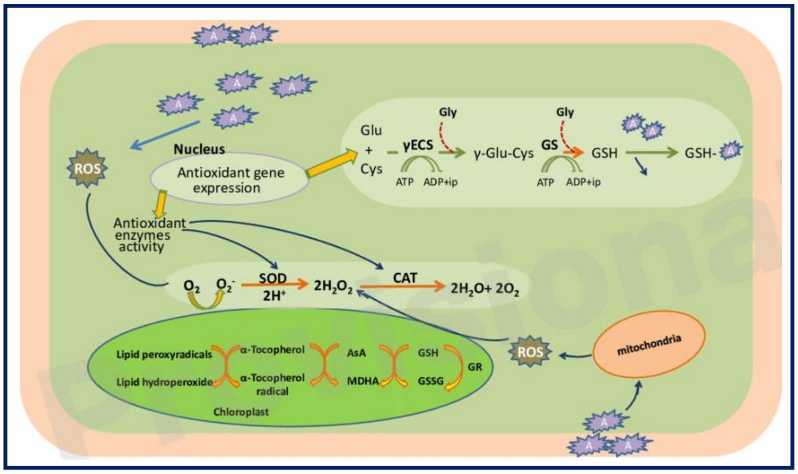

Fig. 42: Illustrates Heavy metal induced-oxidative stress, tolerance and detoxification mechanisms in the plant cell. AsA; 2521 ascorbic acid, CAT; catalase, Cys; cysteine, c-ECS; c-glutamylcysteine synthetase, Glu; glutamine, Gly; glycine, 2522 GR; glutathione reductase, GS; glutathione synthetase, GSH glutathione (reduced), GSSG; oxidized glutathione, H2O2; hydrogen peroxide, MDHA; monodehydroascorbate, O2; oxygen molecule, O2 •‾ 2523 ; superoxide radicals, ROS; 2524 reactive oxygen species, SOD; superoxide dismutase, A; heavy m*et al.,* After Singh *et al.,* (2015).

Arsenic is known as the most poisonous metalloid Zangi and Filella (2012), but under normal environmental conditions, it does not show its straight toxicity because of the higher intracellular phosphate level Zangi and Filella (2012). In the case of plant growth and development, As has no essential role Dixit *et al.,* (2016); Singh *et al.,* (2015). The forms of As and their toxicity may vary from species to species Farooq *et al.,* (2016). As induces oxidative stress, and along with this, it disturbs the redox state, which damages the membranes, proteins thereby eventually leading to cell death Dixit *et al.,* (2016); Srivastava *et al.,* (2007); Srivastava *et al.,* , (2011). At elevated As level, crop yield, seed germination, biomass production are reduced Abedin and Meharg, (2002) Fig. (43).

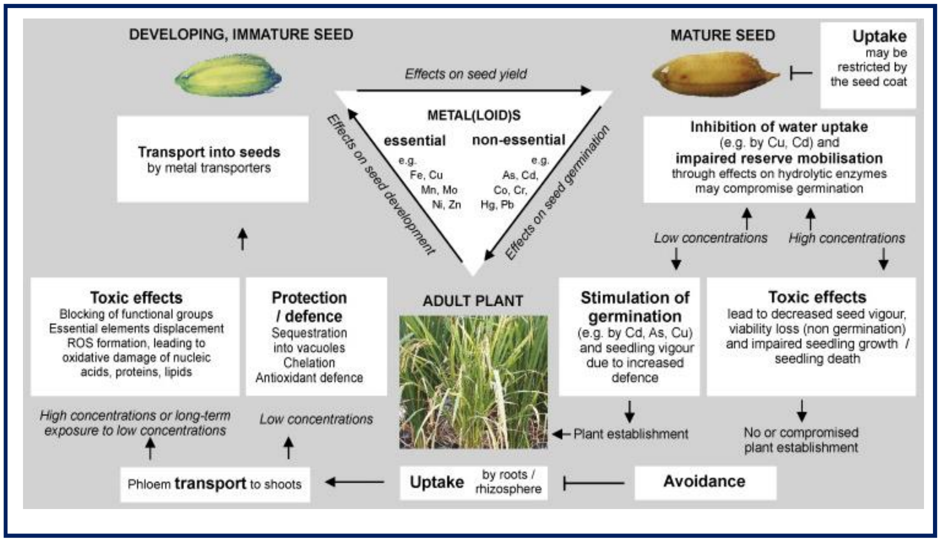

Fig. 43: Summarizing the effects of metals and metalloids on seeds; the images of Oryza sativa (rice) are used to represent seeds and plants generally. After Kranner and Colville, (2011).

Inhibitor effects of as have been observed on the germination of seeds in several crop plants, such as in rice Hossain, *et al.,* (2007), wheat Zengin, (2012), and some vegetables Dutta, Islam, & Mondal, (2014). Many of the other effects of Asare plant height reduction Jahan *et al.,* (2003), decreased root and shoot growth Carbonell-Barrachina *et al.,* (1998); Cox *et al.* (1996), as well as photosynthetic rate Dutta and Mondal, (2014). Additionally, As causes panicle sterility in rice Dutta and Bandopadhyay, (2016). Earlier studies showed that the significant toxicity of arsenate is related to the inhibition of NAD+ reduction, mitochondrial respiration, as well as ATP formation Zangi and Filella, 2012). When plants uptake arsenate, it is transformed to arsenite by the activity of reductase enzymes. So it can be said that in plants the toxicity of As (V) may be due to its conversion into As (III) Farooq *et al.,* (2016). As (III) toxicity is mainly because of the formation of covalent bonds with narrowly spaced thiolate and imidazolium nitrogens, Fig. (44). Thus, the cysteine residue containing the active sites of enzymes and receptors can be affected with consequences on disulfide bond formation, essential to maintain the tertiary structure of a protein Zangi and Filella, (2012). According to some studies, As (III) interacts with many proteins, comprising cytoskeleton protein filaments, DNA repair enzymes, transcriptional regulators, and nicotinic receptors Fig. (45).Hoffman and Lane, (1992); Kitchin andWallace, (2008); Li and Broome, (1999); Menzel *et al.,* (1999); Zangi and Filella, (2012), Zhang *et al.,* (2007).

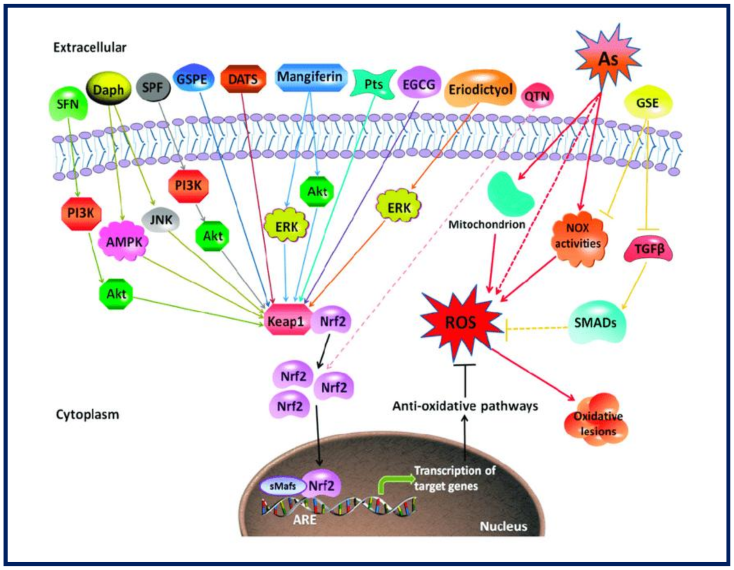

Fig. 44: Illustrates a mechanism of protective effects against arsenic-induced toxicity by antioxidants extracted from plants. The representative natural antioxidants extracted from plants show various mechanisms for protection against arsenic-induced toxicity. Most of them (SFN, Daph, SPF, GSPE, DATS, mangiferin, Pts, EGCG, and eriodictyol) promote the dissociation of Nrf2 with Keap1, promoting the expression of downstream genes of Nrf2, and finally increasing the antioxidant capacity. QTN is suggested to act though Nrf2 without clear evidence. Additionally, GSE protects against arsenic-induced oxidative damage through suppression of NOX-mediated ROS generation. SFN, sulforaphane; Daph, daphnetin; SPF, Sorbus pohuashanensis flavonoids; GSPE, grape seed proanthocyanidins extract; DATS, diallyl trisulfide; Pts, pterostilbene; EGCG, (-)- pigallocatechin-3-gallate; GSE, grape seed extract; TGFβ, transforming growth factor-β; NOX, Nicotinamide adenine dinucleotide phosphate oxidase; SMADs, drosophila mothers against decapentaplegicprotein. After Hu *et al.* (2020)

These proteins are inactivated when As combines with them. As (III) also causes alterations in the methylation pattern of DNA, Chen *et al.,* (2004); Zangi and Filella, (2012); Zhong and Mass, (2001). It was revealed that Sb (III) is more noxious in comparison to Sb (V) Gebel, (1997), Zangi and Filella, (2012). However, in current years, the accumulation and toxicity of Sb in plants have acquired much attention Directive, (1976); Murciego *et al.,* (2007); Feng *et al., (*2011).

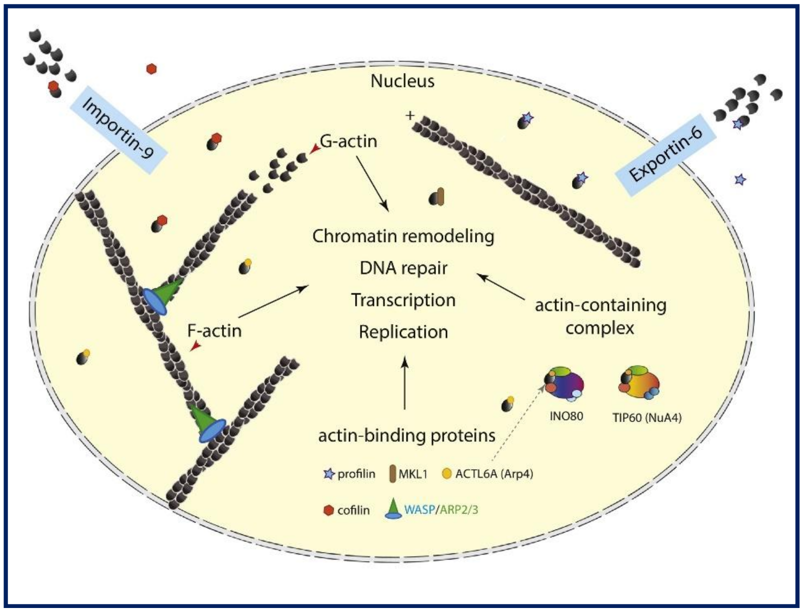

Fig. 45: Illustrates an action in the Nuclear Compartment. Actin is actively imported into the nucleus by importin-9 and is exported by exportin-6. In the nucleus, actin binds to diverse proteins incorporated into larger complexes like chromatin remodelers. Nuclear actin filaments form in a situation- and species-specific manner Baarlink *et al., (*2017), Bohnsack *et al., (*2006) and may bind the nuclear pore Caridi *et al., (*2018). F-Actin, Min and Defea (2011)].After Hurst etal (2019)

In plant tissues, 5–10 mg kg^{-1} Sb is reported to be phytotoxic Feng *et al.,* (2011); Kabata-Pendias, (2010); however, Eikmann and Kloke (1993) reported that 5 mg Sb kg^{-1} in plants is tolerable. Exposure to both trivalent and pentavalent forms of Sb in rice (*Yuhong No.1*) was reported to inhibit growth, reduced yield and the sprout rates of its seeds and, along with this, it also reduces the transformation ratios of dry matter Feng *et al.,* (2011); He and Yang, (1999). In recent times, it has been found that the accumulation of Sb in plant tissues induces oxidative damage and reduces the biomass of Microlepia hancei and Cyclosorus dentatus Feng *et al.,* (2011), Feng, etal (2009). The toxic amount of B affects the vegetative growth of the plant Fang *et al.,* (2016). B toxicity reduces cell division in the roots Liu *et al.,* (2000), affects cell wall expansion and the growth of shoots and roots. It also lowers chlorophyll levels in leaves and, consequently the photosynthetic rates. It affects also the levels of lignin and suberin contents Herrera-Rodríguez *et al.,* (2010); Nable *et al.,* (1997), Reid, (2007). At the reproductive stage of plants, B toxicity has an effect on flowering, as well as fruit and seed development Herrera-Rodríguez *et al.,* (2010). B adversely affects the productivity and quality of crops such as Citrus in various areas of the world Cervilla, Blasco *et al.,* (2007); Huang *et al.,* (2014); Miwa *et al.,* (2007); Nable *et al.,* (1997); Papadakis, etal,(2003), the concentration of B in soil and plant tissues is considered to be extremely crucial for yield as well as productivity Nable *et al.,* (1997); Yıldırım, (2017). The characteristic visible symptom of B toxicity among several plant species is leaf burn, either chlorotic or necrotic patches, commonly found at the tips and margins of older leaves Huang *et al.,* (2014); Nable *et al.,* (1997). Plant tolerance to B toxicity varies significantly among plant species Chen, *et al.,* (2012); Huang *et al.,* (2014); Nable, *et al.,* (1997); Reid and Fitzpatrick, (2009a, 2009b), and is usually attributed to reduced deposition of B. Consequently, the efflux of B from the roots occurs Huang, *et al.,* (2014); Nable, *et al.,* (1997). An enhancement in ROS formation in tobacco García *et al.,* (2001), tomato Cervilla *et al.,* (2007, 2009) and chickpea Ardıc *et al.,* (2009) because of B toxicity has been noticed. Only little pieces of information are available about the toxic effects of B on aquatic plants and how it plays a significant role in the ecosystem by providing nutrients to animals at higher trophic levels. Exposure of B even at a low level can show toxicity in aquatic ecosystems, which causes acute health damage, as well as ecosystem damage worldwide, but mainly in Australia, United States, North Africa, and Turkey Gür *et al.,* (2016); Kabay *et al.,* (2007). B toxicity is also known as the main reason for the retardation of root growth, and Aquea *et al., (*2012) have noticed the molecular basis for the root growth retardation in Arabidopsis. They also reported that toxicity enhanced the expression of genes involved in ABA signalling, as well as in ABA response and modification in the cell wall. It also suppresses the expression of genes involved in water transport. Toxicity of B activates water stress response Huang, *et al.,* (2014). Thus, detoxification methods for metalloids are essential at the tissue level to reduce their toxicity Pandey et al., (2019). Polyamines are low molecular weight metabolites that are reported to be associated with the detoxification of As Bohnert *et al.,* (1995); Garg and Singla, (2011); Groppa *et al.,* (2001). They can bind to DNA, as well as to phospholipids. Therefore, they can stabilize the nucleus and membrane functions Garg and Singla, (2011), Groppa *et al.,* (2001). P. vittata uptakes high amount of As from the soil Garg and Singla, (2011); Ma, *et al.,* (2001); Smith *et al.,* (2010), thereby favouring the growth of other plants. Hyper-accumulation is hence considered a mechanism for detoxification. Ferrous plaque is known to co-precipitate with elements such as As Feng *et al.,* (2013); Liu *et al.,* (2006), Ca, Cu, Zn and P Feng, *et al.,* (2013), Jiang, *et al.,* (2009). It has been reported that Fe plaques can sequester a large amount of Sb, and hence it reduces the uptake of Sb, and this phenomenon has been published in rice Feng *et al.,* (2013); Huang *et al.,* (2012); Okkenhaug *et al.,* (2012). Many of the studies showed that the addition of Si and Se externally could reduce the uptake of Sb and ameliorate the Sb-toxicity in the crop plants Feng *et al.,* (2013).

10. Functional depiction of Metal-Toxicity-Related Genes

In recent years, transcriptomic analyses have focused on the integrated response of several metals and metalloids, which cooperate in plants under stress. The main purpose of these analyses has been to unveil the mechanisms that are shared among plants to cope with different toxic and non-toxic elements present in the soil, and to determine the form in which toxic elements take advantage of existing metal transporters and liberate chelating compounds, allowing them to enter the plant cell. Another aspect of this type of analysis is the translocation or accumulation of toxic elements within the different complex cell structures that make up plant roots. Furthermore, the use of technologies such as microarrays, RNAseq, and wide genome analysis has increased the amount of transcriptomic and genomic information available for plants under metal stress Li *et al.,* (2017), Xu *et al.,* (2020), Tian *et al.,* (2021). When analyzing the different plant transcriptome under conditions of metal/metalloid stress, conserved trends have been observed. In fact, upregulated genes reported in different articles can be classified based on their Gene Ontology (GO) outputs in five main categories: metabolic pathways, organic acids, transporters, phytohormones, and ROS production Fig. (46).The results observed in these categories might vary according to the plant species, developmental stage, environmental conditions, the type of metal/metalloid to which the plant is been exposed, its concentration, and whether the plant is sensitive/tolerant or hyper accumulative.

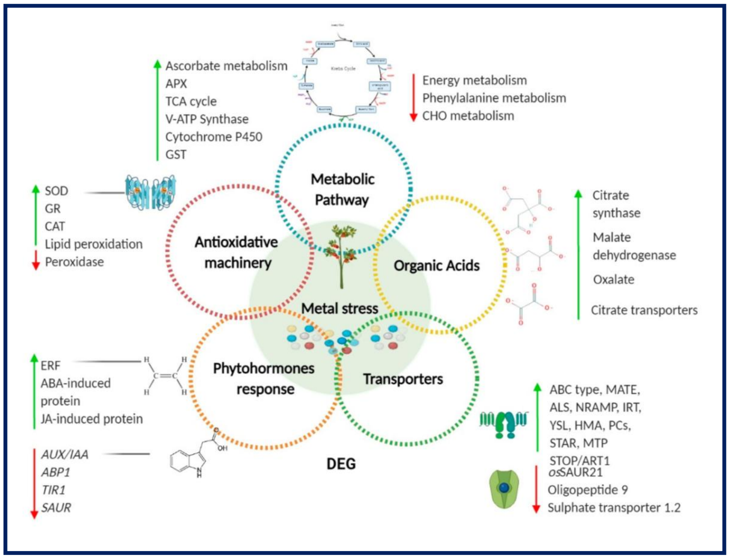

Fig. 46: Illustrates General diagram of the Gene Ontologies (GOs) of up- and downregulated genes under different metal stress conditions in plants by transcriptomic analysis. Venn diagram showing the differentially expressed genes (DEGs) up-(green arrow) and down- (red arrow) regulated that belong to the GOs of reactive oxygen species (ROS) production and antioxidative machinery, transporter-like genes (plasma membrane or vacuoles), metabolic pathways (such as the TCA cycle, which provides OAs) and Phytohormonal genes in responses to As(V), Cd, Pb, and other metals. Colored circles: heavy metals, CHO: carbohydrates, TCA: tricarboxylic acid, APX: ascorbate peroxidase, ERF: Ethylene Response Factor, AUX/IAA: Auxin/Indole-3-Acetic Acid, ABP1: Auxin binding protein 1, TIR1: Transport inhibitor response 1, SAUR: small auxin upregulated RNA, OsSAUR21: auxin-responsive SAUR gene family member of Oryza sativa. After Angulo-Bejarano *et al.,* (2021)

As expected, many of the differentially expressed genes (DEGs) are involved in the antioxidative machinery Huang *et al.,* (2019), Xu *et al.,* (2017), Han *et al.,* (2019), Nunes-Nesi *et al.,* (2014), transport, Xu *et al.* (2020), Wang etal (2020), Huang *et al.* (2014), and cell wall biosynthesis Zhao *et al.,* (2020).Therefore, the expression (constitutive or metal stress induced) of such genes is vital for the plant, mostly in the roots during the first stages of metal stress. The localization of some transporter-like genes within the cell structure (plasma membrane or vacuoles) provides knowledge of which mechanisms are preferred by plants at the molecular level Yokosho *et al.,* (21014), Zhu *et al.,* (2021), among the main upregulated metabolic pathways, the upregulation of the TCA cycle is one of the common features of plant metal stress tolerance Fig. (47).

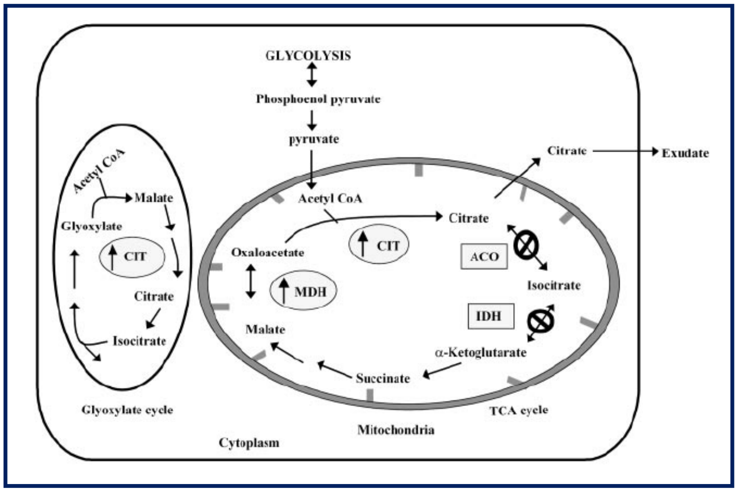

Fig. 47: Illustrates metabolic map of TCA and glyoxylate cycles, indicating positions of genes that could be modulated for altering citrate metabolism. Up-regulation of genes involved in citrate synthesis and down-regulation of genes involved in citrate catabolism (Ø) would enhance citrate synthesis and/or its accumulation in cells. After Anoop *et al.,* (2003).

Further, the oxidative environment provided by the alteration in mitochondrial functions (transmembrane potential impairment) causes an increase in membrane permeability, activating members of the programed cell death machinery, such as the caspase-3-like pathway Nunes-Nesi *et al.,* (2014). The TCA cycle provides citrate and malate, which are heavy metal and metalloid chelators that are liberated by the plant as part of the first defense strategies upon contact with the toxic element Nunes-Nesi *et al.,* (2014), The overproduction of ROS, overall mitochondrial dysfunction, and the upregulation of antioxidant enzymes such as GST, SOD, CAT, and peroxidase, among others, are common responses in plants from different phylogenic backgrounds Fig. (48).

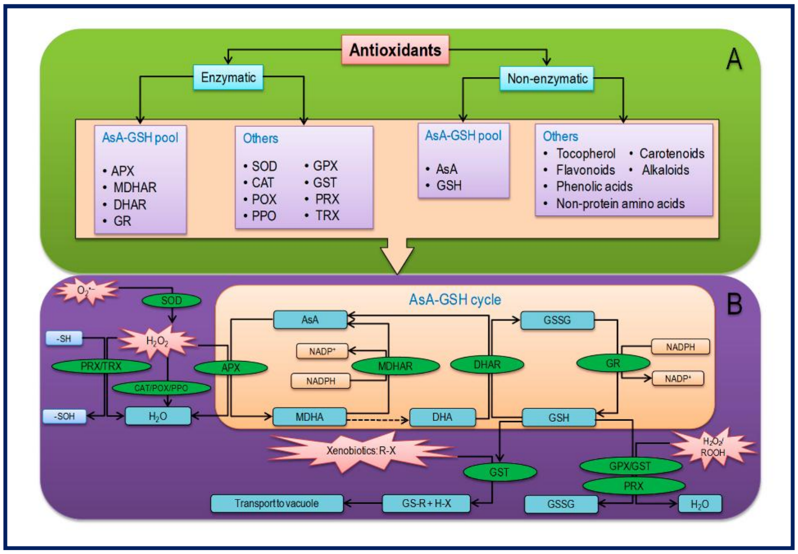

Fig. 48: Illustrates the overview of plant antioxidant defense system: (A) types of antioxidants and (B) combined mechanisms of enzymatic and nonenzymatic antioxidants. See the text for a more detailed description. APX, ascorbate peroxidase; AsA, ascorbate; CAT, catalase; DHA, Dehydroascorbate; DHAR, Dehydroascorbate reductase; GPX, glutathione peroxidase; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; GST, glutathione S-transferase; H2O2, hydrogen peroxide; MDHA, monodehydroascorbate; MDHAR, monodehydroascorbate reductase; NADPH, Nicotinamide adenine dinucleotide phosphate; O2 •−, superoxide anion; POX, peroxidases; PRX,

peroxiredoxins; R, aliphatic, aromatic, or heterocyclic group; ROOH, hydro peroxides; –SH, thiolate; SOD, superoxide dismutase; –SOH, sulfonic acid; TRX, thioredoxin; X, sulfate, nitrite, or halide group. After Hasanuzzaman *et al.,* (2020).

Hasanuzzaman *et al.,* (2020) reported that antioxidants directly or indirectly scavenge ROS and/or control ROS production Carocho, and Ferreira (2013). The antioxidant defense system consists of low-molecular-weight nonenzymatic antioxidants and some antioxidant enzymes Hasanuzzaman *et al.,* (2019). The nonenzymatic antioxidants such as AsA, GSH, α-tocopherol, phenolic compounds (PhOH), flavonoids, alkaloids, and no protein amino acids work in a coordinated fashion with antioxidant enzymes such as SOD, CAT, POX, polyphenol oxidase (PPO), APX, MDHAR, DHAR, GR, GPX, GST, TRX, and PRX in order to inhibit overproduction of ROS Fig.(49) Nath *et al.,* (2018), Laxa *et al.,* (2019). The catalytic reaction of enzymatic and nonenzymatic antioxidants and the reaction sites in cellular organ. In plants, the enzyme SOD is directly related to stress, which initiates the first line of defense, converting O2 •– into H_2O_2 Biczak (2016), Del Río *et al.,* (2018). This generated H_2O_2 can be further converted into H_2O by the enzymes CAT, APX, GPX, or catalyzed in the AsA-GSH cycle. In plant cell, the AsA-GSH cycle or Asada—Halliwell cycle.

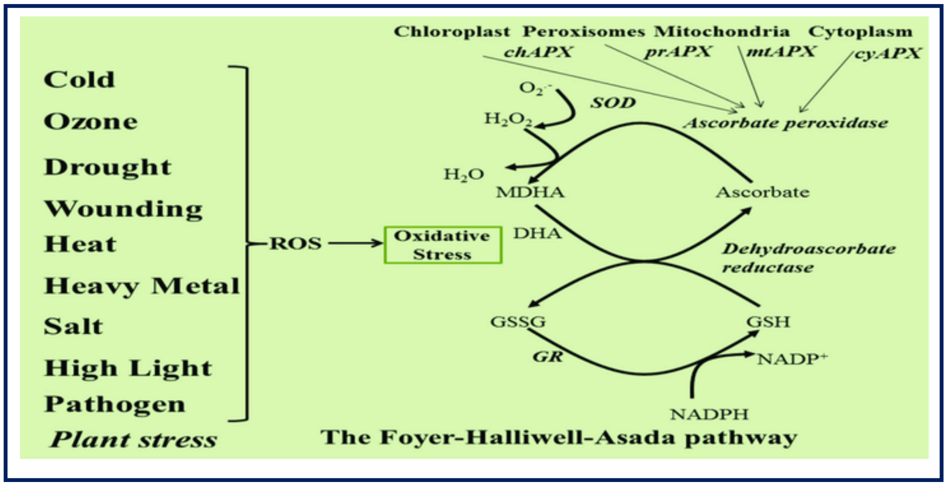

Fig. 49: Illustrates schematic representation of Foyer-Halliwell-Asada Pathway. After Pandey *et al.,* (2017)

The major antioxidant defense pathway to detoxify H_2O_2, which consist nonenzymatic antioxidants AsA and GSH as well as four important enzymes APX, MDHAR, DHAR, and GR. In the antioxidant defense system, a key role is performed by the AsA-GSH cycle to minimize H_2O_2 and redox homeostasis Hasanuzzaman *et al.,* (2019), Fotopoulos *et al.,* (2010). In addition, GPX and GST are also vital enzymes for the detoxification of H_2O_2 and xenobiotics Hasanuzzaman *et al.,* (2018). The major antioxidant defense pathway to detoxify H_2O_2, which consist nonenzymatic antioxidants AsA and GSH as well as four important enzymes APX, MDHAR, DHAR, and GR. In the antioxidant defense system, a key role is performed by the AsA-GSH cycle to minimize H_2O_2 and redox homeostasis Hasanuzzaman *et al.,* (2019), Fotopoulos *et al.,* (2010). In addition, GPX and GST are also vital enzymes for the detoxification of H_2O_2 and xenobiotics Hasanuzzaman *et al.,* (2018). Among nonenzymatic antioxidants, AsA and GSH are the most abundant solubleantioxidants in higher plants Foyer and Noctor (2019), those play a vital role as electron donors and scavenge ROS directly through AsA-GSH cycle Hasanuzzaman *et al.,* (2019). Moreover, beta-carotene reacts with •OH, O_2 •–, and ROO• radicals resulting in reduced cellular ROS concentrations Kapoor *et al.,* (2019).

This indicates that the response mechanism of plants during metal toxicity or tolerance is highly conserved Huang *et al.,* (2019), Han *et al.,* (2019), and Yamamoto *et al.,* (2002). For example, when Al enters the mitochondria, it alters the electron transport chain, decreasing ATP production and thus increasing ROS production Li and Xing (2010). Additionally, enzymes that are fundamental for the TCA cycle are upregulated under metal stress; accordingly, the presence of citrate synthase, malate dehydrogenase, and malic enzyme, among others, has been reported Han *et al.,* (2015), Sun *et al.,* (2014), Yadav (2010). In a study on *F. esculentum* conducted by our research group, we were able to identify, through a microarray analysis, the upregulation of TCA-cycle-related enzymes (citrate synthase, NAD-dependent malic enzyme 2) under Al-induced stress. PCS1 was also upregulated. In *F. esculentum and F. tataricum* ,a set of important transport-related genes Yokosho *et al.,* (2014), Zhu *et al.,* (2014). As expected from previous studies, FeALS1, FeMATE1, and FeMATE 2 were upregulated in *F. esculentum*. A comparison of these two closely related species at the genome-wide level revealed conserved tolerance mechanisms and the upregulation of FtFRD genes (FtFRDL1 and 2) and ART-Like genes (ARL1 and 2) among other genes Zhu, *et al.* (2014).

Recently, a transcriptomic analysis of *F. tataricum*leaves in response to Pb tolerance indicated that most of the DEGs were grouped into cell wall, binding, and energy metabolism functions. Five genes were evaluated in a yeast model, among them Metal Transporter Protein C2 (MTPC2), phytochelatin synthetase-like family protein (PCSL), a vacuolar cation/proton exchanger 1a (VCE1a), NRAMP3, and phytochelatin synthetase (PCS). All of them helped to increase the Pb tolerance in the yeast model Wang *et al.* (2020) Fig. (50).

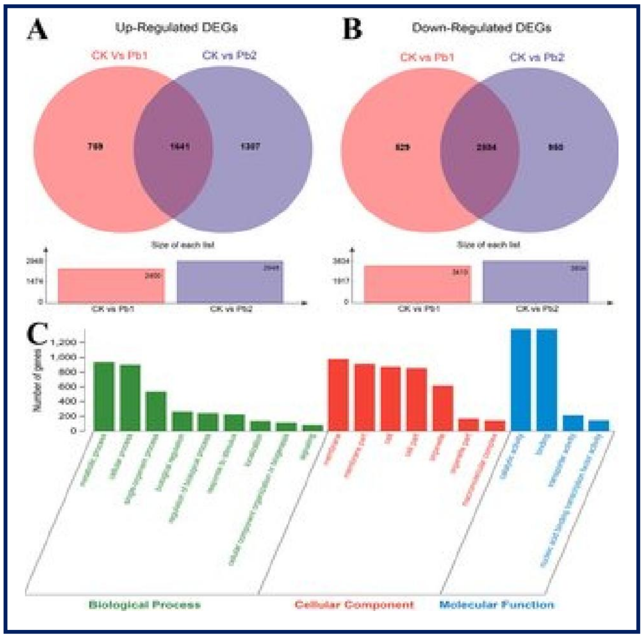

Fig. 50: Illustrates 3 Venn diagram of differentially expressed genes (DEGs) for CK vs Pb1 and CK vs Pb2 and Gene Ontology classification of DEGs. a) Upregulated DEGs for CK vs Pb1 and CK vs Pb2; (b) Downregulated DEGs for CK vs Pb1 and CK vs Pb2; (c) GO classification of DEGs for CK vs Pb1 and CK vs Pb2. The x-axis represents GO terms belonging to three categories; the y-axis represents the gene numbers for each term. After Wang *et al.,* (2020)

The first transcriptomic research analysis in plants under conditions of metal stress or tolerance focused on identifying the main transporters (ABC transporters, NRAMPs, and STARs, among others) that help plant cells to internalize and compartmentalize toxic ions or to excrete organic acids (citrate, malate, etc.) Dubey *et al.,* (2014), Wang *et al.,* (2014), Gao *et al.,* (2015). However, interest in the role of secondary-metabolism-derived compounds is increasing; for example, commonly found DEG accessions correspond to chalcone synthase, phenylpropanoids, flavonoids, and terpenes Li *et al.,* (2017) Xu *et al.,* (2017). Additionally, an increase in the role of ABA signaling is gaining interest; for example, in *S. orientalis* L., the mechanistic model presented after the transcriptomic analysis of this plant under conditions of Cd stress revealed that ABA could play a role in gene expression, which, in turn, activates transcription factors and response elements in the nucleus, directing the plant transcription process to the synthesis of antioxidant enzymes (GSH, CAT, or peroxidase), and at the same time, triggering phenylpropanoid biosynthesis, leading to an increase in cell wall compounds Xu *et al.,* (2020) Fig.(51).

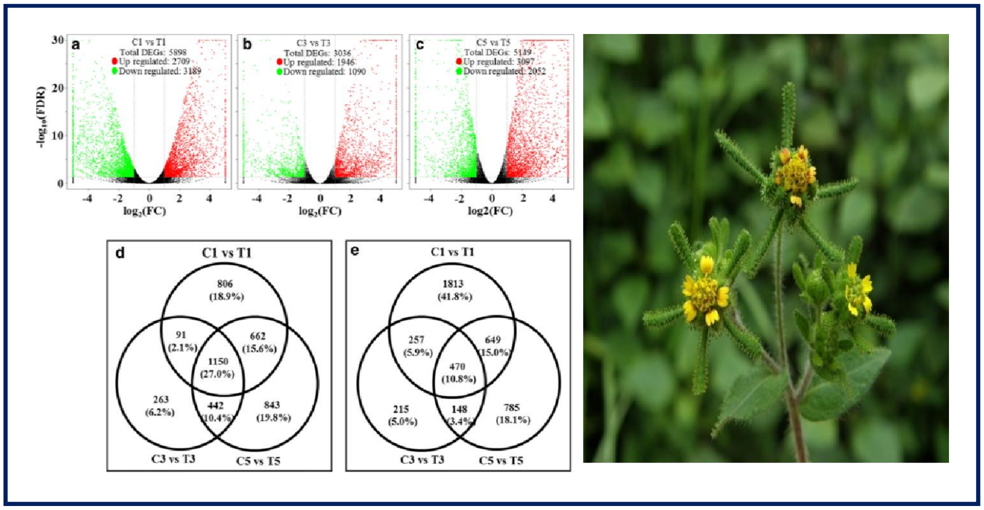

Fig. 51: Illustrates differentially expressed genes (DEGs) of *Siegesbeckia orientalis* roots under cadmium stress at three time points. (**a** – **c**) DEGs between the control and treatment at each time point. FDR, false discovery rate. FC, fold change. (**d**) Venn diagram of upregulated genes among three comparisons. (**e**) Venn diagram of downregulated genes among three comparisons. After Xu *et al.,* (2020)

Xu *et al.,* (2020) stated that *Siegesbeckia orientalis L.*was identified as a novel Cd-hyperaccumulator and valuable phytoremediation material. However, the molecular mechanisms underlying Cd accumulation in S. orientalis are largely unknown. In this study, RNA-Seq analysis was performed to study the Cd-accumulating mechanisms in its roots with or without Cd treatment. The RNA-*Siegesbeckia orientalis* L. analysis generated 312 million pairs of clean reads and 78G sequencing data. De novo transcriptome assembly produced 355,070 transcripts with an average length of 823.59 bp and 194,207 unigenes with an average length of 605.68 bp. Comparative transcriptome analyses identified a large number of differentially expressed genes in roots under Cd stress, and functional annotation suggested that *Siegesbeckia orientalis* L. utilizes various biological pathways involving many gene networks working simultaneously to cope with the stress. This study revealed that four biological pathways were mainly involved in *Siegesbeckia orientalis* L. tolerance to Cd stress, including reactive oxygen species scavenging, phenylpropanoid biosynthesis pathway, Cd absorption and transport, and ABA signaling pathway. The genes related to photosynthesis and heavy metal transport are likely the potential candidates and could be further investigated to determine their roles in Cd tolerance in *Siegesbeckia orientalis* L. roots. These findings will be useful to understand the Cd accumulation mechanisms in *Siegesbeckia orientalis* L. and facilitate the study of phytoremediation at the molecular level in plants.

Fu *et al.,* (2020) stated that similarly was reported in case of C. sinensis, where epigallocatechin gallate and polymeric proanthocyanidins were found to be part of secondary metabolites that form complexes with Al ions as part of the resistance machinery in tea plants. Regarding terpene biosynthesis, this can also be deregulated because of toxic metals in the environment. A transcriptomic analysis of *F. arundinacea* revealed several unigenes that are directly related to terpene biosynthesis: monoterpenes, sesquiterpenes, diterpenes, carotenoids, brassinosteroids, and zeatin. In fact, limonene and pinene degradation related genes were found to be upregulated in the Pb-hyper accumulative variety, whereas in the Pb-tolerant variety, the deregulation of carotenoid biosynthesis and zeatin biosynthesis related enzymes was observed by Li *et al.,* (2017). Plants also respond to heavy metal or metalloid stress by increasing the levels of important plant phytohormones, such as auxins, SA, gibberellins, brassinosteroids, Strigolactones, ethylene, and ABA, due mainly to their role as important plant chemical messengers for both biotic and abiotic stressors. Several studies have indicated that their exogenous application onto plants undergoing metal/metalloid stress has a positive effect by restoring some of the metabolic functions lost or decreased under stress.However, the exact mechanism of how metal/metalloid stress triggers alterations in auxin distribution, mainly in the root apices, is not fully understood. Nevertheless, investigations that suggest that metals such as Cu, Cd, and Al can exert changes to auxin distribution patterns and auxin homeostasis-related genes also are distinctly altered in plant roots under stress Wang *et al.,* (2014), Singh *et al.,* (2021). An overall increase in metal/metalloid toxic compounds above the tolerance threshold generates an immediate response in plants. Depending on the plant species and many other factors, some of them could organize the defense against these compounds or ions, avoiding as much harm as possible at both the metabolic and molecular levels. Metals such as Cu inhibit the expression of auxin biosynthetic and catabolic genes and inhibit root elongation, affecting the meristematic and elongation zones. Cu can, in turn, modulate auxin distribution Hu *et al.,* (2013). The interesting results that can be obtained by means of transcriptomics, wide genome association mapping, and more recently, metabolomics, phenomics, and ionomics will help us to understand how plants prepare themselves and change under different environmental conditions, which is a fascinating example of the plants' genomes, transcriptome, and metabolome plasticity. This contributes to the understanding of metal/metalloid stress in plants and the mechanisms involved at the genetic level. Furthermore, can be utilized to discover the behavior of hyper accumulative plants, which can be employed for biotechnological purposes with the goal of phytoremediation to reduce, the increasing metal and metalloid concentrations in soil.

11. Conclusion and Prospects

Anthropogenic activities, along with natural erosion, have resulted in increased concentrations of metalloids in the environment. The metalloids have severely affected agriuujjcultural land and ecosystems. As a result, a decline in crop production and ever-increasing flow of toxic metalloids in the food chains are becoming imminent. Uptake of metalloids occurs via passive, that is, simple diffusion or facilitated diffusion or active route necessitating metabolic energy. Transport processes are essential for the influx of metals and minerals from the soil to different plant organs, as well as for the efflux of toxic compounds produced inside the cell. Different metalloids require different membrane proteins for the uptake and efflux and they vary from genus to genus. As it is known that arsenic is very toxic to plants, it is necessary to inhibit its uptake. The uptake of As (V) and As (III) mainly occurs via phosphate transporters and aquaporins, therefore modulation of phosphate transporters and aquaporins with the aid of genetic engineering might assist in the alleviation of As toxicity. The uptake mechanism of Sb (V), a harmful metalloid, is not well understood, so it is a prerequisite to elucidate the uptake mechanism of Sb (V) for mitigating its toxic effects on crop plants. Modifications to the availability and distribution of metalloids that function as plant nutrients or the presence of toxic, no biological metals in soil induce various adaptive mechanisms in plants (uptake and exclusion transporters, OAs, enzymatic and oxidative responses, and chelators), highlighting the importance of these molecules within plants in response to abiotic stress. Through the examples reviewed here, we inferred a high degree of specialization among plants. Such capacity must certainly have been obtained through evolution; however, more recently domesticated crops must face rapid adaptation to the growing areas of contaminated soils. Nevertheless, as has occurred with noncrop plants, studies have confirmed their capability to utilize these essential elements (as transporters and translocation machinery) to diminish metal/metalloid stress. A common trend amongst all the given examples is the use of pre-existing transporters by the plant to introduce toxic compounds into sites of accumulation inside the plant cell. Such a phenomenon takes place on the natural barrier between the plant cell and the rhizosphere: the plant cell wall. Changes could occur in this cell barrier under conditions of metal/metalloid toxicity. The prospective use of these technologies in the environment can help to ameliorate the rise of soil pollution in different areas around the world. Therefore, it is vital to continue this type of applied research using the scientific basis provided by both physiological and omic approaches to propose a solution to the decrease of arable land in vast areas of our planet due to soil acidification and contamination. The knowledge gathered from these findings can help to increase the production and yield of staple crops such as maize, rice, and wheat. Additionally, the use of alternative cycles between economically important agronomic crops and those with phytoremediation capacity should be used. Biotechnological tools, such as the use of byproducts and transgenic crops for phytoremediation, are now considered important strategies to overcome soil pollution and meet the demands for arable land worldwide for the next generations

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