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Supplementation of Selenium and Its Nano on Crop Plant Tolerance and Physiological Responses: A Review

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ABSTRACT

Selenium is an essential micronutrient that enhanced plant growth and development in trace amounts. It also protects plants against different abiotic stresses by acting as an antioxidant or stimulator in a dose-dependent manner. Selenium can also enhance cellular functions like membrane stability, mineral nutrition homeostasis, antioxidant response, photosynthesis, and thus improve plant growth and development under metal/metalloid stress. Selenium uptake, translocation, and accumulation is crucial to achieving the inclusive benefits of selenium in plants. Plant growth is affected by various abiotic stresses, including water, temperature, light, salt, and heavy metals. Selenium is not an essential nutrient for plants also but plays an important role in alleviating the abiotic stresses suffered by plants. Selenium promotes the uptake of beneficial substances, maintains the stability of plasma membranes, and enhances the activity of various antioxidant enzymes, thus alleviating adverse effects in plants under abiotic stresses. Therefore, we discusses the absorption, translocation, and signaling of selenium in plants as well as proteomic and genomic investigations of selenium shortage and toxicity. Low concentrations of selenium can mitigate metal/metalloid toxicity in plants and improve tolerance in various ways. Selenium stimulates the biosynthesis of hormones for remodeling the root architecture that decreases metal uptake. Growth enhancing function of selenium has been reported in a number of studies, which is the outcome of improvement of various physiological features. Photosynthesis has been improved by selenium supplementation under metal/metalloid stress due to the prevention of pigment destruction, sustained enzymatic activity, improved stomatal function, and photosystem activity However, extra amounts of selenium can restrict metal uptake by roots and translocation to shoots, which is one of the vital stress tolerance mechanisms. Metal/metalloid toxicity decreases crop productivity and uptake of metal/metalloid through food chain causes health hazards. Modulating the antioxidant defense, system selenium mitigates oxidative stress of selenium that improving the yield and quality of plants. However, excessive concentration of selenium exerts toxic effects on plants.

Keywords: abiotic stress, biofortification, heavy metals, phytoremediation, plant nutrition, oxidative stress, xenobiotics

1.Introduction

1.1. Selenium element (Se)

Metalloids encompass a group of chemical elements that are found widespread in nature (Bienert *et al.,* 2008). Bhattacharjee *et al.* (2008) reported that most of their physical and chemical characteristics are intermediate between metals and non-metals element. Physically, they are glittery, fragile with intermediate electric conductivity similar to metals, and chemically they behave as nonmetals. Metalloids possess intermediate amphoteric, electronegative values and ionization energies. They have an ability to form an alloy with metals. The number and identities of metalloids are determined based

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on the criteria used for their classification, which includes electronegativity, packing efficiency, the Goldhammer–Herzfeld ratio, atomic conductance, and bulk coordination number. Among them, electronegativity is the commonly used criterion to categorize metalloids. Mann *et al.* 2000; Vernon (2013) stated that most of the metalloids possess electronegative values ranging from 1.8 to 2.2, packing efficiencies between 34 and 41%, and the Goldhammer–Herzfeld ratio of 0.85–1.1

As plants and environments are intensively connected, they face multifaceted stresses due to their sessile nature. Feng *et al.* (2020) stated that rapid industrialization and agricultural development, plenty of wastewater, fertilizers, and pesticides are discharged that result in toxic metal/metalloid contamination of soil and other environmental components Fig. (1).

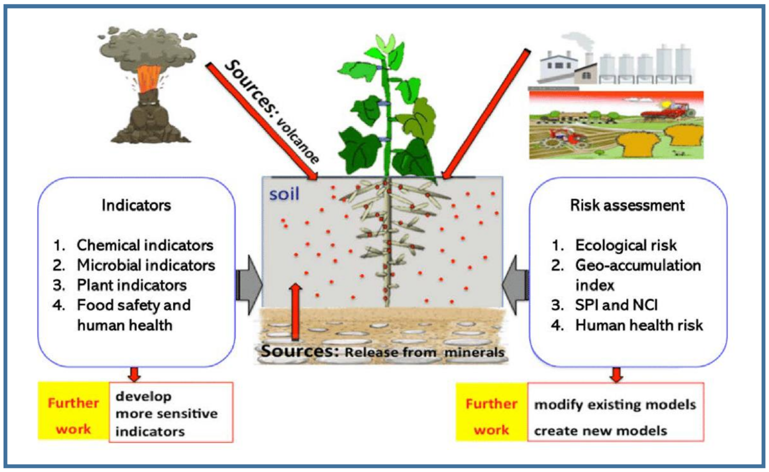


Fig. 1: Illustrates the map of framework on future management of soil pollution. SPI represents Single-factor index and NCI represents Nemero comprehensive index. After Xin *et al.,* (2022)

Xin *et al.* (2022) reported that soil pollution caused by potentially toxic metals has become a worldwide environmental issue. Geogenic processes and anthropogenic activities are two important sources of soil pollution. Soils may inherit toxic metals from parent materials; however, soil pollution mostly results from industrial and agricultural activities. Contamination by metals can be indicated by the changes in chemical, biochemical, and microbial properties of soils and plant responses. The total concentration of toxic metals in soil is still the most widely used indicator for risk assessment although extractable amounts have been reported to be more closely related to plant uptake. Several models have been proposed for assessing soil contamination by toxic metals, but none of them is commonly accepted for application to a wide range of soils. We highlights how toxic metal contamination negatively affects soil and environmental quality, affects food quality and security, and poses a threat to human health. Further research is needed to not only improve soil contamination diagnosis, metal dealing, and regulatory standards but for remediation efficiency.

Exposure of plants to various metals and metalloids causes the alteration of physiological and biochemical processes by higher metal uptake and translocation, thereby hampering the normal growth and development of the plant. In addition, these unrest the cellular metabolic functions by binding with proteins, nucleic acids, and enzymes (Hasanuzzaman *et al.,* 2019) Fig. (2).

Angulo-Bejarano *et al.* (2021) stated that Worldwide, the effects of metal and metalloid toxicity are increasing, mainly due to anthropogenic causes. Soil contamination ranks among the most important factors, since it affects crop yield, and the metals/metalloids can enter the food chain and undergo bio magnification, having concomitant effects on human health and alterations to the environment. Plants have developed complex mechanisms to overcome these biotic and abiotic stresses during evolution. Metals and metalloids exert several effects on plants generated by elements such as Zn, Cu, Al, Pb, Cd, and As, among others. The main strategies involve hyperaccumulation, tolerance, exclusion, and chelation with organic molecules. Recent studies in the omics era have increased knowledge on the plant genome and transcriptome plasticity to defend against these stimuli. The aim of the present review is to summarize relevant findings on the mechanisms by which plants take up, accumulate, transport, tolerate, and respond to this metal/metalloid stress.

The antioxidant properties of selenium, which promote heavy metal detoxification and metabolism at adequate concentrations, encourage plant growth and development (Shekari *et al.,* 2019; Gui *et al.,* 2022). Selenium has been referred to as a "two-edged sword" and an "essential poison" since it may be damaging to living things at both deficient and excess levels (Gupta and Gupta 2017; Reilly 1996). Selenium protects plants from oxidative damage by improving antioxidative activities. It also boosts glutathione peroxidase (GSH-Px) activity, which helps plants to resist stress and aging. Moreover, selenium can also help plants to withstand abiotic stress by reducing the enormous amount of free radicals that plants release under stress conditions.

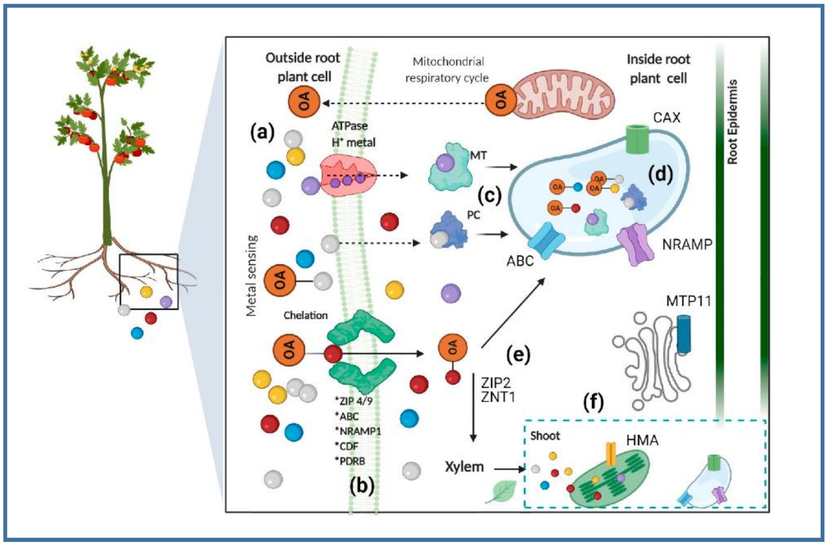


Fig. 2: Schematic representation of the physiological and molecular processes of absorption/translocation of metals into plants. The uptake of heavy metals ((e.g., Pb, Cd, As, Zn, etc.) (Colored circles)) Occurs through the root cells, where the presence or high concentration of these metals triggers 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. Figure 1. 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.

The addition of Selenium can boost protein synthesis by directly influencing it through amino acid forms that include Se substituted sulfur and can stimulate the synthesis of chlorophyll by controlling the biosynthesis of porphyrins in plants. Porphyrins are reported to have a role in the synthesis of chlorophyll (Lidon *et al.,* 2018; Yang *et al.,* 2022; Zhao *et al.,* 2022) Fig.(3).

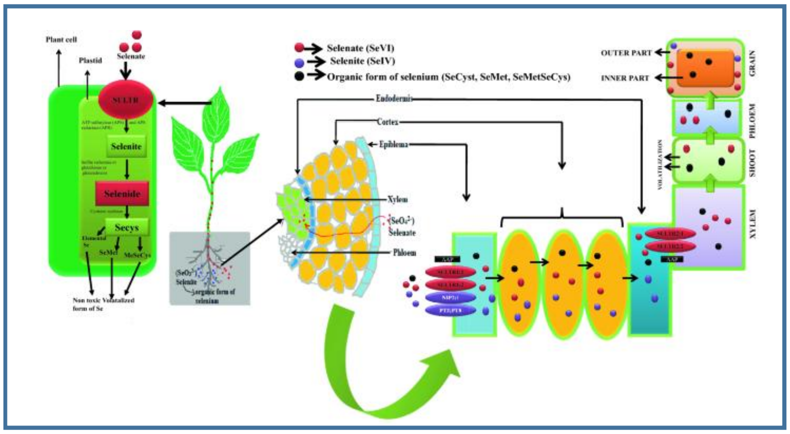


Fig. 3: A fow diagram showing the transporters responsible for carrying various selenium species through the xylem and phloem to the leaves and grains. Selenate (SeVI) and selenite (SeIV) are taken up by sulphate transporters (SULTR1;1, SULTR1;2) and aquaporins (NIP2;1), respectively. The phosphate transporters PT2 and PT8, respectively also take up Se (IV). SULTR2;1 and SULTR2;2 aid in the direct transport of selenium (Se(VI)) into shoot cells and also aid in the loading of selenium (Se(VI)) into xylem in plants. By the amino acid permease AAP1, organic Se species are also absorbed by plant roots and transported up to grains. The volatile form of selenium is called dimethyldiselenide. Phloem is used to carry selenium into seeds. It has been observed that several Se species can be found in various layers of seed. After Khan *et al.,* (2023)

Khan *et al.* (2023) stated that many nations have adopted the application of selenium and biofortification techniques in recent years to reduce abiotic stress and produce selenium-enriched food. However, further in-depth knowledge of selenium metabolism, signaling, and selenocompound activities in plants is required to achieve its desired effects. It is obvious that the form and concentration of selenium are crucial for maximizing its benefits. Additionally, research on nano conjugates containing SeNP may pave the way for improved positive impacts on plants. To sustain agriculture, future studies should focus on determining how selenium and the nano form of Selenium impact plants with regard to their speciation and metabolites. When selenium level surpasses the safety threshold, Selenium-induced superoxide radical ($O^{2.-}$) accumulation can harm cell membranes or create non-specific selenoproteins Fig. (4) .

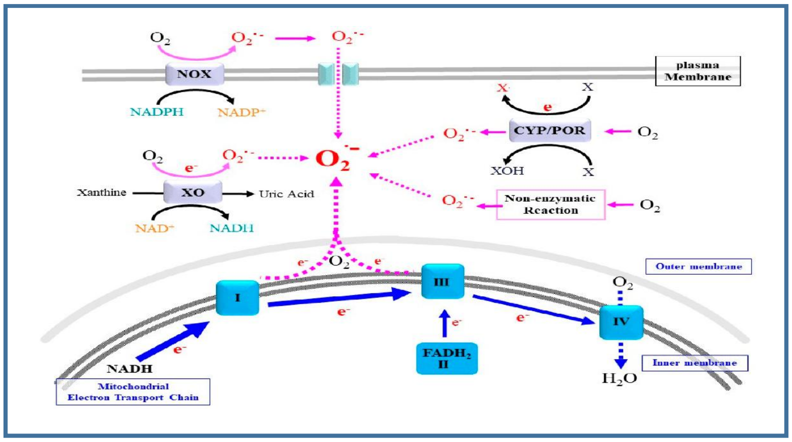


Fig. 4: Representative electron sources of superoxide. While mitochondrial ETC is the major source for superoxide ($O^{2.-}$), many enzymes, such as NADPH oxidase (NOX), xanthine oxidase (XO), and cytochrome P450 (CYP)/cytochrome P450 reductase (POR), convert molecular oxygen to superoxide either as a main product or as a byproduct during oxidation of a variety of compounds (X), such as benzene compounds, drugs, and steroid hormones. Superoxide is also produced non-enzymatically. After Fujii *et al.,* (2022)

Fujii *et al.* (2022) reported that superoxide is a primary oxygen radical that is produced when an oxygen molecule receives one electron. Superoxide dismutase (SOD) plays a primary role in the cellular defense against an oxidative insult by ROS. However, the resulting hydrogen peroxide is still reactive and, in the presence of free ferrous iron, may produce hydroxyl radicals and exacerbate diseases. Polyunsaturated fatty acids are the preferred target of hydroxyl radicals. Ferroptosis, a type of necrotic cell death induced by lipid peroxides in the presence of free iron, has attracted considerable interest because of its role in the pathogenesis of many diseases. Radical electrons, namely those released from mitochondrial electron transfer complexes, and those produced by enzymatic reactions, such as lipoxygenases, appear to cause lipid peroxidation. While GPX4 is the most potent anti-ferroptotic enzyme that is known to reduce lipid peroxides to alcohols, other antioxidative enzymes are also indirectly involved in protection against ferroptosis. Moreover, several low molecular weight compounds that include α-tocopherol, ascorbate, and nitric oxide also efficiently neutralize radical electrons, thereby suppressing ferroptosis. The removal of radical electrons in the early stages is of primary importance in protecting against ferroptosis and other diseases that are related to oxidative stress.

Schiavon *et al.* (2012), foliar reported that wilting and shoot stunting are two indicators of selenium phytotoxicity selenium has dangerous consequences on plants at higher concentrations, including reduction of nutrient uptake. It may be due to changes in the permeability coefficient of certain ions in biofilms Nawaz *et al.* (2015). Moreover, selenium can interact with minerals in tissues and upset the mineral balance in plants. Particularly, when selenium concentration is too high, the antioxidant effect is changed into a pro-oxidant. A High concentration of selenium can lead to the accumulation of reactive oxygen species (ROS) and subsequently oxidative stress, which can induce malfunction in the photosynthesis process Fig. (5).

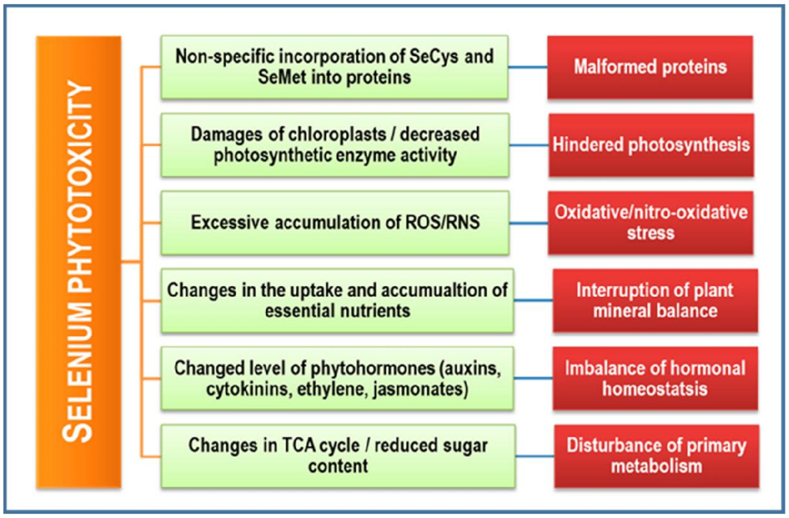


Fig. 5: Figure 4. A schematic representation of the causes an A schematic representation of the causes and consequences of Se toxicity in plants. After Hasanuzzaman *et al.,* (2020)

Hasanuzzaman *et al.* (2020) stated that selenium is a widely distributed trace element with dual (beneficial or toxic) effects for humans, animals, and plants. The availability of selenium in the soil is reliant on the structure of the parental material and the procedures succeeding to soil formation. Anthropogenic activities affect the content of selenium in the environment. Although plants are the core source of selenium in animal and human diet, the role of selenium in plants is still debatable. A low concentration of selenium can be beneficial for plant growth, development, and ecophysiology both under optimum and unfavorable environmental conditions. However, excess selenium results in toxic effects, especially in selenium sensitive plants, due to changing structure, function of proteins, and induce oxidative/nitrosative stress, which disrupts several metabolic processes. Contrary, selenium hyperaccumulators absorb and tolerate exceedingly large amounts of selenium, could be potentially used to remediate, i.e., remove, transfer, stabilize, and/or detoxify selenium-contaminants in the soil and groundwater. Thereby, selenium -hyperaccumulators can play a dynamic role in overcoming global problem selenium -inadequacy and toxicity. However, the knowledge of selenium uptake and metabolism is essential for the effective phytoremediation to remove this element. Moreover, selecting the most efficient species accumulating selenium is crucial for successful phytoremediation of a particular selenium -contaminated area. This review emphasizes selenium toxicity in plants and the environment about selenium biogeochemistry and phytoremediation aspects.

In addition to this, a higher concentration of selenium can cause plant photosystem reaction centers to shut down, lowering the rates of photosynthesis (Zhang *et al.,* 2014; Gupta and Gupta 2017). Numerous studies have noted the role of defense-related phytohormones in the development of selenium resistance in plants Szőllősi *et al.,* (2022). The expression of several ethylene and/or jasmonic acid (JA) responsive genes was elevated by selenate treatment in a transcriptome investigation to find selenate-responsive genes. Selenite-treated plants also showed induction of many of these same ethylene and/or JA-responsive genes. Application of selenite stimulates the gene PDF1.2, which encodes a plant defense that is induced when the ethylene and JA pathways are simultaneously activated. As evidence that these genes are selenium-regulated, transgenic AOS promoter: GUS and PDF1.2 promoter::GUS plants showed GUS activity in the leaves of selenite-treated plants but not in the leaves of untreated plants (Tamaoki *et al.,* 2008).

The obvious effect of metal stress is the stimulation of reactive oxygen species (ROS) generation, which causes the oxidative stress by damaging cellular macromolecules including lipids, protein, and DNA.The ultimate extreme levels of metal/metalloid can lead to plant death (Hasanuzzaman *et al.,* 2020). Contrarily, plants possess the defense tactics for keeping ROS at a nontoxic level to regulate its signaling roles through involving non-enzymatic and enzymatic antioxidants (Hasanuzzaman *et al.,* 2019). Toxic metal contamination in the environment also causes threats to human health via the food chain (Feng *et al.,* 2020). Therefore, much attention should be given for inducing higher metal stress tolerances of plants for increasing worldwide crop production along with reducing health hazard. For aiming this, thirst of researchers is to develop technology or management practice, which will help to reduce metal uptake in plants in contaminated soil. Consequently, the use of chemical approaches, especially essential micronutrients like selenium, has become one of the effective strategies to mitigate the toxic effects of metals because of its biochemical functions (Wang *et al.,* 2020). It is beneficial in regulating plant growth and development by alleviating environmental stress-induced damage when applied at a low concentration (Ismael *et al.,* 2019).

Particularly, selenium supplementation can restrict metal absorption by roots and translocation to shoots, which is one of the vital metals/metalloid stress tolerance mechanism (Hasanuzzaman *et al.,* 2020). Besides, selenium-induced improvement in cellular functions and membrane stability, mineral nutrition with upregulation of antioxidants response, and metabolites function and also reduction of oxidative stress in plants has been widely explored against metal stresses (Gupta and Gupta, 2017; Zhao *et al.,* 2019; Wang *et al.,* 2020). Such roles of selenium at low dose in plant growth as antioxidants, stress alleviators, and uptake inhibitor of metals, including Cd Luo *et al.,* (2019), Cr Ulhassan *et al.,* (2019), Pb Wu *et al.,* (2016), As Shahid *et al.,* (2019), Cu Trevisan *et al.,* (2011), Hg Tran *et al.,* (2018), etc. have been reported already. Additionally, lower selenium concentration is able to stimulate the biosynthesis of hormone-like auxin, which causes the remodeling of root architecture with higher root growth for resulting in lower metal uptake (Feng *et al.,* 2020). Supplementation of selenium causes an increase of pectin and hemicellulose contents as well as thickness of cell wall, which enhances the binding of toxic metals by the cell wall (Zhao *et al.,* 2019). Selenium can regulate the subcellular distribution of metals. Moreover, exogenous selenium application in various major crops including rice, lettuce, cucumber, Brassica, etc. significantly has been reported to reduce metal accumulation with growth improvement, which also ensures better crop productivity and health benefits to consumers Pandey and Gupta, (2018). It is also reported that, excessive concentration of selenium is also toxic for plants by causing chlorosis, growth reduction, and even oxidative stress Molnár *et al.,* (2018); Hasanuzzaman *et al.,* (2020); that is why it is imperative to emphasize selecting the optimal dose of selenium. Therefore, extensive and broad scale research is still required for determining the crucial dose and engagements of selenium for attaining plant tolerance toward metals. The potentiality of selenium for reducing metal toxicity in plants through various strategies, including restriction of metal uptake, regulation of ROS metabolism, responses of antioxidants, and ion homeostasis, which are associated with the improvement of plant physiology, growth, development, and yield has been gathered, which will be supportive to get insight into selenium-induced metal tolerance in plants. Mashabela *et al.* (2023) stated that plants undergo metabolic perturbations under various abiotic stress conditions; due to their sessile nature, the metabolic network of plants requires continuous reconfigurations in response to environmental stimuli to maintain homeostasis and combat stress.

The comprehensive analysis of these metabolic features will thus give an overview of plant metabolic responses and strategies applied to mitigate the deleterious effects of stress conditions at a biochemical level. In recent years, the adoption of metabolomics studies has gained significant attention due to the growing technological advances in analytical biochemistry (plant metabolomics). The complexity of the plant biochemical landscape requires sophisticated, advanced analytical methods. As such, technological advancements in the field of metabolomics have been realized, aided much by the development and refinement of separatory techniques, including liquid and gas chromatography (LC and GC), often hyphenated to state-of-the-art detection instruments such as mass spectrometry (MS) or nuclear resonance magnetic (NMR) spectroscopy. Significant advances and developments in these techniques are briefly highlighted in this review. The enormous progress made thus far also comes with the dawn of the Internet of Things (IoT) and technology housed in machine learning (ML)-based computational tools for data acquisition, mining, and analysis in the 4IR era allowing for broader metabolic coverage and biological interpretation of the cellular status of plants under varying environmental conditions Fig. (6). Thus, scientists can paint a holistic and comprehensive roadmap and predictive models for metabolite guided crop improvement.

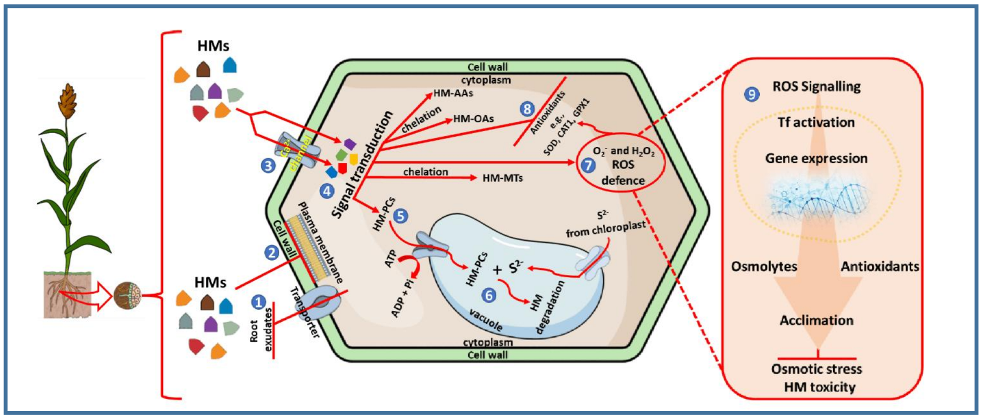


Fig. 6: Schematic representation of plants' response to heavy metals and induced osmotic stress. Plants growing in HM-contaminated soils can prevent HM uptake by (1) releasing root exudates that form insoluble complexes with metal ions, and (2) reduction of metal influx across the plasma membrane. Metal ions influx can still occur through the Ca2+ channels and the plasma membrane into the plant cell (3), MAPK-mediated signal transduction (4), occurs to induce the expression of metal chelating ligands in the cytosol to form complexes such as HM-AAs (amino acids), HM-OAs (organic acids), HM-MTs (metallothioneins) and HM-PCs (phytochelatins). HM-PC complexes are transported through the tonoplast into the vacuole by ATP-binding-cassette and V-ATPase transporter (5), which are further complex with sulfides from the chloroplast for degradation (6). The perception of HMs is amplified by the signalling transduction to induce ROS defence and oxidative stress (7), this leads to the activation of antioxidants (8) and (9) to combat oxidative damage, osmotic stress, and HM toxicity. After Mashabela *et al.,* (2023)

1.2. Selenium nanoparticle (Se-NP)

Over elemental Selenium, selenium nanoparticles (Se NP) have a larger advantage. Se NP is more bioactive and has enhanced solubility than bulk Se (Zahedi *et al.,* 2019). Se NP is introduced as a stable nano form of Selenium for application as a stress modulator and fertilizer in agricultural crops (Djanaguiraman *et al.,* 2018). The application of NPs alters the signaling pathways dependent on ROS, which controls plant growth by enhancing antioxidant activity and chloroplast functionality (Mittler, 2017) Fig. (7).

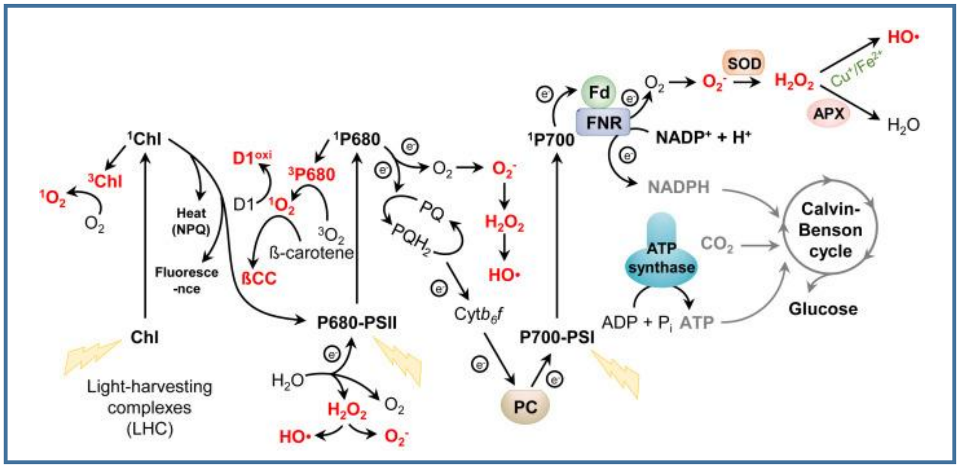


Fig. 7: ROS metabolism in the chloroplast. The light energy captured in the photosystem II (PSII) light-harvesting antenna complex (LHC) drives photosynthetic electron transfer. Upon absorption of light energy, the chlorophyll (Chl) molecule converts to the singlet-state Chl (1 Chl). Part of the excess energy is re-emitted as fluorescence or dissipated as heat, a process referred to as non-photochemical quenching (NPQ). Alternatively, the spontaneous decay of 1 Chl results in triplet excited state 3 Chl with an increased lifespan (Muller *et al.,* 2001). 3 Chl is quenched by carotenoids in the LHC, returning to its ground state. Otherwise, 3 Chl transfers the absorbed energy to the ground state of O2, producing 1 O^{-2}. The LHC-generated 1 O^{-2} can also be quenched by carotenoids. Energy that reaches the PSII RC Chl (P680) from the antenna complex also leads to the formation of 1 O^{-2} via 3 P680 when the electron (e$^-$) transfer chain becomes over-reduced.1 O^{-2} then oxidizes b-carotene and D1 proteins in its vicinity. H_2O_2 and O_2 can be generated through two-electron oxidations of H_2O at the electron donor side of PSII and a one-electron reduction of O2 at the acceptor side of PSII, respectively. The subsequent conversion of H_2O_2 and O_2 into other forms of ROS is described in Pospisil (2009). PSI is also involved in the production and detoxification process of O_2 and H_2O_2. The photosystem I (PSI) electron acceptor ferredoxin (Fd)- NADP+ oxidoreductase (FNR) transfers electrons from ferredoxin to NADP+ to produce NADPH. NADPH and ATP produced by ATP synthase are used to produce glucose as the final product of photosynthesis via the Calvin–Benson cycle. To maintain PSII in a partly oxidized form under conditions in which the electron transfer chain becomes over-reduced, FNR transfers an electron to O2, thereby generating O2$^-$. O2$^-$ is further converted into H_2O_2 by SUPEROXIDE DISMUTASEs (SODs). ASCORBATE PEROXIDASEs (APXs) then contribute to H_2O_2 scavenging through the ascorbate–glutathione cycle (Apel and Hirt, 2004). OHd is generated via the Fenton reaction by the interaction of H_2O_2 with reduced transition metal ions such as Fe^{2+} and Cu$^+$. bCC, b-cyclocitral; PQH2, plastoquinone; PQ, oxidized form of plastoquinone; Cytb6f, cytochrome b6f complex; PC, plastocyanin. After Mengping and Chanhong Kim (2021).

Mengping and Chanhong Kim (2021) reported that chloroplasts overproduce reactive oxygen species (ROS) under unfavorable environmental conditions, and these ROS are implicated in both signaling and oxidative damage. There is mounting evidence for their roles in translating environmental fluctuations into distinct physiological responses, but their targets, signaling cascades, and mutualism and antagonism with other stress signaling cascades and within ROS signaling remain poorly understood. Great efforts made in recent years have shed new light on chloroplast ROS-directed plant stress responses, from ROS perception to plant responses, in conditional mutants of Arabidopsis thaliana or under various stress conditions. Some articles have also reported the mechanisms underlying the complexity of ROS signaling pathways, with an emphasis on spatiotemporal regulation. ROS and oxidative modification of affected target proteins appear to induce retrograde signaling pathways to maintain chloroplast protein quality control and signaling at a whole-cell level using stress hormones. This review focuses on these seemingly interconnected chloroplast-to-nucleus retrograde signaling pathways initiated by ROS and ROS-modified target molecules. We also discuss future directions in chloroplast stress research to pave the way for discovering new signaling molecules and identifying intersectional signaling components that interact in multiple chloroplast signaling pathways.

Moreover, the application of Se NP has been reported to improve the nutrient value of fruits (Mittler 2017). Other benefits of Se NP over elemental Selenium form include decreased toxicity, higher glutathione peroxidase, thioredoxin reductase activity, and excellent catalytic efficiency (Wang *et al.,* 2007). According to reports, the biological activity and antioxidative properties of Se NP are inversely and directly correlated with particle size and the ratio of surface area to volume (Nandini *et al.,* (2017); Djanaguiraman *et al.,* 2018). Furthermore, Shahverdi *et al.* (2010) discussed the antifungal properties of SeNP. They also noted that while elemental Selenium is less hazardous to plants at lower concentrations than selenate or selenite, it is physiologically inert and insoluble in water at redox state zero Wang *et al.,* (2007). However, Se NP can be used in place of Bulk Se (B-Se) because it has the same beneficial properties as BSe and is soluble in water, and not hazardous to plants at the same concentration. In an experiment done on tobacco (*Nicotiana tabacum*), Domokos-Szabolcsy *et al.* (2012) discovered that the application of Se NP and selenate promoted root growth. Additionally, tobacco organogenesis was enhanced; but the application of Selenium at higher concentrations impeded the processes. However, Se-NP at the same concentration did not show harmful effects as Selenium. The most significant characteristic of NP is that it can generate more results with fewer applications as compared to its bulk form. Se NP appears to be an effective antioxidant and reduce agricultural pollution and chemical contamination (Ali *et al.,* 2020; Ahmad *et al.,* 2016). Thus, the application of Se NP is predicted to lead to more sustainable, profitable, and eco-friendly growth of agriculture. However, the use of Se NP for the benefit of plants is still in its infancy, and additional research is required to fully exploit this potential.

2. Nano selenium and its prospects in agriculture

Nanoparticles (NPs) act as a bridge between bulk and molecular structures. The nano form of selenium has a number of benefits over other forms of selenium, due to its size, porosity, surface area, bio-dispersion, reactivity, and mobility inside the plants (Bisht *et al.,* 2022) Fig. (8). The application of selenium is reported to modulate physiological responses in agricultural crops. This method does possess several limitations where the application of SeNP may overcome those limitations due to its outstanding properties (Djanaguiraman *et al.* 2018). SeNP is reported to possess similar efficacy to selenium in up-regulating seleno enzymes in agricultural crops (Zhang *et al.,* 2005). It has been hypothesized that applying SeNP will override selenium's toxic properties and have a more positive impact on agricultural crops due to their biosafety and bioactivity properties Fig.(8,9). Se NP can be synthesized either by chemical or green methods. In addition to this, the NP produced by photosynthesis or green methods has minimal defects and a homogenous chemical composition (Kalita *et al.,* 2021).

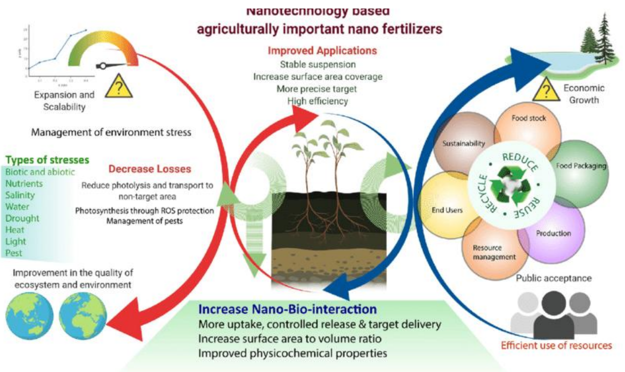


Fig. 8: Nanotechnology-based agriculturally important nano fertilizers increase agronomic productivity, efficiency, and reduce environmental stress. Efficient utilization of nanotechnology in agriculture for future sustainability. After Mittal *et al.,* (2020).

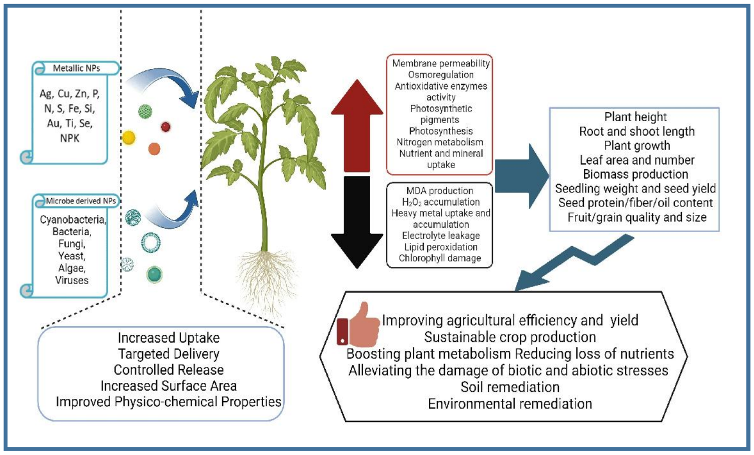


Fig. 9: Nanotechnology-based agriculturally important nano fertilizers increase agronomic productivity, efficiency, and reduce environmental stress. Efficient utilization of nanotechnology in agriculture for future sustainability. After Goyal *et al.,* (2023)

Goyal *et al.* (2023) reported that nanotechnology is revolutionizing agricultural technology by unlocking new frontiers of innovation. It allows for enhanced nutrient delivery, precise pest and disease management, improved soil health, and optimized resource utilization. The intricate manipulation of matter at the nano-scale level offers a toolkit of novel solutions, paving the way for sustainable and resilient food production systems in the face of evolving challenges and global demands. It might boost agricultural productivity by establishing an improved complementary interaction between the consumption of chemicals and stability in the environment. In the near future, it might be used as cutting-edge science to address the dilemma of worldwide malnutrition. Sophisticated nano-technological tools for innovative agriculture could result in increased output with lower expenditure on goods and services. In order to treat plant diseases and reduce crop loss, nanotechnology has made it more convenient to produce modern, effective agricultural products for plants, including nano-fertilizers, nano-biofertilizers, and nanopesticides. Even though there is a plethora of literature on particular nanoparticles, the extent of the toxicity of numerous nanoparticles remains uncertain.

As a result, the potential uses of such substances are restricted because of the dearth of comprehension of risk evaluations and impacts like toxicity, bioaccumulation, water and soil contamination, biodiversity impact, and disruption of ecosystem functions. Unintended consequences and regulatory challenges add to the concerns about the well-being of humans and other life forms. International regulatory and legal collaborations are required to fully utilize this modern technology, diligent database, and monitoring design. Nanotechnology in agriculture, particularly nano-fertilizers and nano-biofertilizers, offers a promising future. Advanced delivery systems for fertilizers and nutrients, such as nano-carriers and nano-capsules, can be explored. The involvement of nanoparticles in precision agriculture techniques, including IoT sensors (the Internet of Things) and data analytics, holds immense potential. The sustainability and environmental impact of nanoparticles with long-term effects on soil health, water quality, and biodiversity need to be assessed. The development of novel targeted soil and crop-specific hybrid nanoformulations as fertilizers and pesticides with cost-benefit analysis requires consideration.

3. Selenium assimilation by plants

Plants metabolize Selenium via the sulfur metabolic system because of the chemical similarity of the two elements (Feng *et al.,* 2021) Fig. (10).

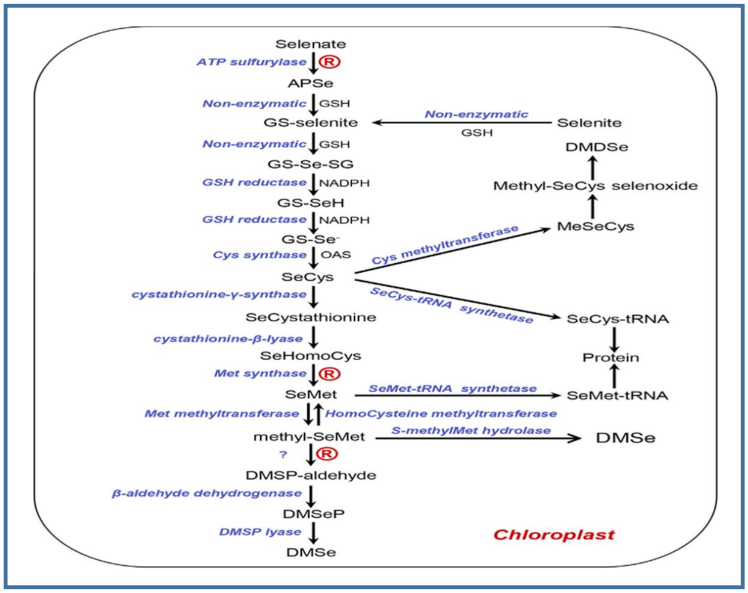


Fig 10: The sulfate assimilation and metabolism pathway. Enzymes are indicated in orange letters. Abbreviations of metabolites: APS, adenosine 5′-phosphosulfate; PAPS, 3′-phosphoadenosine 5′-phosphosulfate; R-OH, hydroxylated precursor; Ser, serine; OAS, *O*-acetylserine; Cys, cysteine; OPH, *O*-phosphohomoserine; Thr, threonine; Cyst, cystathionine; Hcyst, homocysteine; Met, methionine; γ-EC, γ-glutamylcysteine; GSH, glutathione; GS-X, glutathione conjugate; Glu, glutamate; X-Cys Gly, cysteinylglycine conjugate. Abbreviations of enzymes: ATPS, ATP sufurylase; APK, APS kinase; SOT, sulfotransferase; APR, APS reductase; SiO, sulphite oxidase; SiR, sulfite reductase; SAT, serine acetyltransferase; OAS-TL, OAS(thiol)lyase; CGS, cystathionine γ-synthase; TS, threonine synthase; CBL, cystathionine β-lyase; MS, methionine synthase; γ-ECS, γ-glutamylcysteine synthetase; GSHS, glutathione synthetase; GST, glutathione-S-transferase; GGT, γ-glutamyl transferase. After Li *et al.,* (2020)

Similar to that of sulfur, the assimilation of Selenium occurs in the cytosol and plastids of plant leaf cells (Becana *et al.,* 2018). Selenate is translocated into the leaves after being taken up by the roots. Selenate is firstly activated by adenosine triphosphate sulfurase to form adenosine 50 -phosphoselenate and continuously reduced by adenosine 50 -phosphosulfate reductase to generate selenite (Jez 2019; Bohrer *et al.,* 2014) Fig. (11). Selenite can be further converted into selenide. The reduction of sulfite into sulfide is achieved by the action of sulfite reductase (SR) during sulfate metabolism (Bekturova *et al.,* 2021). The reduction from selenite to selenide may also be achieved by the action of SR. Subsequently, selenide is further transformed into SeCys under the catalysis of cysteine synthase (White 2018; Sors *et al.,* 2005).

Plants cannot distinguish between SeCys and Cys; thus, SeCys can displace Cys and be non-specifically incorporated into proteins, resulting in protein dysfunction and causing plant toxicity (Trippe, 2021). Some plants retain the capacity to process SeCys into non-toxic forms, thus avoiding selenium toxicity. Part of SeCys is broken down to elemental selenium by the mediation of SeCys lyase. Elemental selenium can be excreted by plant cells, thus declining the Se concentration in the plant body. The other part of SeCys is converted into selenocystathionine by cystathionine-γ-synthase and then into seleno homocysteine by cystathionine-β-lyase. Seleno homocysteine would be transformed into SeMet under the catalysis of Met synthase (Hossain *et al.,* 2021). Plants also can process SeCys and SeMet into nonprotein amino acids. SeCys and SeMet can be converted into methyl SeCys (MeSeCys) and methyl SeMet (MeSeMet) under the mediation of SeCys methyltransferase and S-adenosylL-Met: Met-S-methyltransferase, respectively. This process can reduce the misincorporation of SeCys and SeMet into proteins (White, 2018). MeSeCys and MeSeMet are further converted into volatile dimethyl diselenide and dimethyl selenide. The two volatile compounds would be excreted from plant cells, thereby reducing the selenium concentration in plants and reducing selenium damage to plants (Tagmount *et al.,* 2002; Freeman *et al.,* 2010).

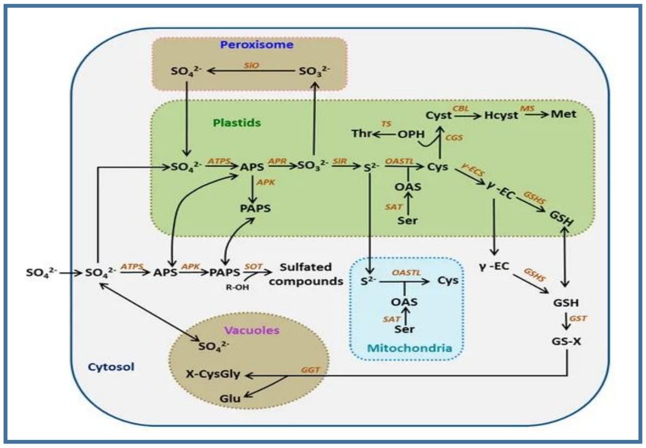


Fig. 11: The metabolism of selenate and selenite in chloroplasts or plastids (Terry *et al.,* 2000). Selenate is first reduced to adenosine 5-phosphoselenate (APSe) by ATP sulfurylase (EC: 2.7.7.4) and then further reduced nonenzymatically to GSH-conjugated selenite (GS-selenite). Selenite is also reduced nonenzymatically to GS-selenite. The GS-selenite is reduced to selenodiglutathione (GS-Se-SG) by GSH, and GS-Se-SG is further reduced to selenol (GS-SeH) by NADPH and subsequently to GSH-conjugated selenide ($GS\text{-}Se^-$) by GSH reductase. SeCys is synthesized from $GS\text{-}Se^-$ and O-acetylserine catalyzed by Cys synthase. SeMet may be synthesized from SeCys via SeCystathionine and SeHomoCys catalyzed by cystathionine-γ-synthase, cystathionine-β-lyase, and Met synthase. SeCys is methylated to methyl-SeMet by Cys methyltransferase. SeMet is methylated to methyl-SeMet, and is further converted into dimethylselenonium propionate (DMSeP) by DMSeP- lyase, and then cleaved to DMSe by S-methylMet hydrolase and volatilized. R represents the rate-limiting step. After Zhang *et al.,* (2022)

4. Selenium and their stresses in plants

4.1. Impact of drought on plant growth and developments

Wahab *et al.* (2023) reported that Drought stress threatens global food security and requires creative agricultural solutions. Recently, phyto-synthesized nanoparticles (NPs) have garnered attention as a way to reduce food crop drought. This extensive research examines how phyto-synthesize improve crop growth and biochemistry in drought-stressed situations. The review begins with an introduction highlighting the urgency of addressing the agricultural challenges posed by drought and the significance of nanoparticles synthesized from photosynthesis in this context. Its purpose is to underscore the importance of sustainable farming practices. This approach is contrasted with conventional methods, elucidating the ecological and economic advantages of phyto-synthesized. Discussing phyto-synthesized nanoparticles, including titanium dioxide, iron oxide, gold, silver, and copper. In addition, we review their ability to enhance crop growth and stress resistance.

The primary focus is to elucidate the effects of phyto-synthesized on plant development under drought stress. Noteworthy outcomes encompass improvements in seed germination, seedling growth, water absorption, photosynthesis, chlorophyll content, the activation of antioxidant defense mechanisms, and the modulation of hormonal responses. These results underscore the potential of phyto-synthesized as agents for enhancing growth and mitigating stress, and assessing the risks and challenges of using phyto-synthesized NPs in agriculture. Considerations include non-target organisms, soil, and environmental impacts. Drought stress occurs in plants with an internal water deficit due to an inadequate water supply. The condition manifests when plants are without sufficient water for an extended period. Plants' physiology, morphology, and productivity can all be drastically altered by drought stress. One significant effect of drought stress is reducing crop yields (Yasmeen *et al.,* 2022; Wahab *et al.,* 2022). Plants cannot carry out their critical physiological functions when deprived of water. The plant's photosynthesis, nutritional uptake, and hormonal balance may all suffer, causing stunted growth, withering, and even death (Yasmeen *et al.,* 2022; Waadt *et al.,* 2022; Tripathi *et al.,* 2022). Drought stress also interferes with many plant processes. Many biological activities, such as cellular respiration, which produces energy, require water. These mechanisms, metabolic activity, and plant health, in general, suffer when water is scarce (Mozafari *et al.,* 2018; Bissoyi *et al.,* 2016). Stomatal apertures, which regulate the exchange of gases and water vapor between the plant and the environment, are similarly affected by drought stress. Increasing transpiration can worsen water shortages caused by this interruption (Paidari and Ibrahim, 2021; Silva *et al.,* 2021).

Drought stress causes plants to adapt physiologically by altering gene expression, accumulating Osmo protectants (such as proline and carbohydrates), and activating stress responsive signaling cascades. These systems can aid plants in dealing with drought stress, but they are usually insufficient to prevent serious crop production decreases (Verma *et al.,* 2021; Virmani *et al.,* 2021). Fig. (12) Understanding the effects of drought stress on plants and the processes disrupted under these conditions is essential for developing solutions to alleviate the detrimental repercussions of drought stress on agriculture and the environment. Understanding the complex mechanisms involved in the drought stress response might help researchers and agricultural practitioners increase crop resilience, enhance water management practices, and guarantee food security in the face of more unpredictable climatic conditions (Van Greuning *et al.,* 2020; Falkenberg *et al.,* 2022).

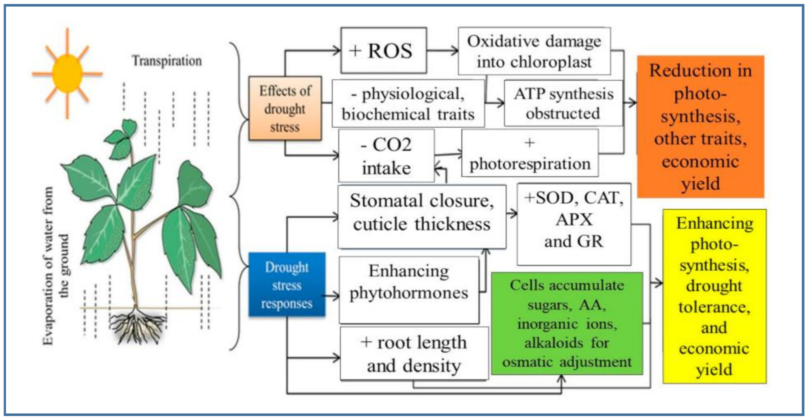


Fig. 12: Adverse effects and adaptations of plants to drought stress, modified from Ullah *et al.,* (2017) (-) means reduce; (+) means increase. After Seleiman *et al.,* (2021)

Seleiman *et al.* (2021) reported that Drought stress, being the inevitable factor that exists in various environments without recognizing borders and no clear warning thereby hampering plant biomass production, quality, and energy. The key important environmental stress occurs due to temperature dynamics, light intensity, and low rainfall. Despite this, its cumulative, not obvious impact and multidimensional nature severely affects the plant morphological, physiological, biochemical and molecular attributes with adverse impact on photosynthetic capacity. Coping with water scarcity, plants evolve various complex resistance and adaptation mechanisms including physiological and biochemical responses, which differ with species level.

The sophisticated adaptation mechanisms and regularity network that improves the water stress tolerance and adaptation in plants are briefly discussed. Growth pattern and structural dynamics, reduction in transpiration loss through altering stomatal conductance and distribution, leaf rolling, root to shoot ratio dynamics, root length increment, accumulation of compatible solutes, and enhancement in transpiration efficiency, osmotic and hormonal regulation, and delayed senescence are the strategies that are adopted by plants under water deficit. Approaches for drought stress alleviations are breeding strategies, molecular and genomics perspectives with special emphasis on the omics technology alteration i.e., metabolomics, proteomics, genomics, transcriptomics, glyomics and phenomics that improve the stress tolerance in plants. For drought stress induction, seed priming, growth hormones, osmoprotectants, silicon (Si), selenium (Se) and potassium application are worth using under drought stress conditions in plants. In addition, drought adaptation through microbes, hydrogel, nanoparticles applications and metabolic engineering techniques that regulate the antioxidant enzymes activity for adaptation to drought stress in plants, enhancing plant tolerance through maintenance in cell homeostasis and ameliorates the adverse effects of water stress are of great potential in agriculture.

Understanding the effects of drought stress on plants and the processes disrupted under these conditions is essential for developing solutions to alleviate the detrimental repercussions of drought stress on agriculture and the environment. Understanding the complex mechanisms involved in the drought stress response might help researchers and agricultural practitioners increase crop resilience, enhance water management practices, and guarantee food security in the face of more unpredictable climatic conditions (Van Greuning *et al.,* 2020; Falkenberg *et al.,* 2022). Fig. (13).

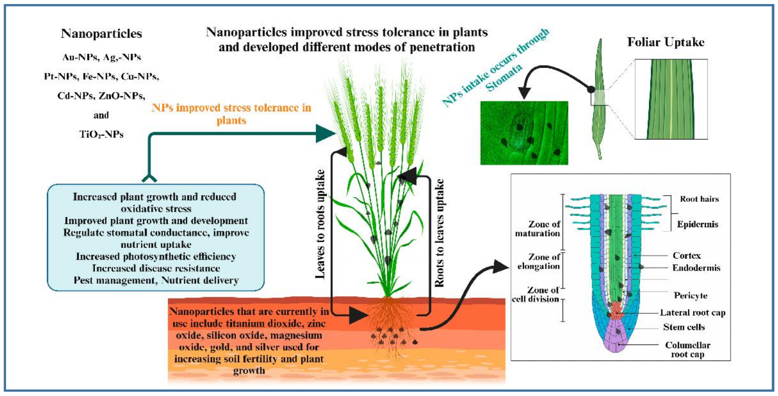


Fig. 13: Nanoparticles improved stress tolerance in plants and developed different modes of penetration. After Abdul Wahab *et al.,* (2023)

Abdul Wahab *et al.* (2023) illustrated that drought stress threatens global food security and requires creative agricultural solutions. Recently, phyto-synthesized nanoparticles NPs have garnered attention as a way to reduce food crop drought. This extensive research examines how phyto-synthesized NPs improve crop growth and biochemistry in drought-stressed situations. The review begins with an introduction highlighting the urgency of addressing the agricultural challenges posed by drought. It also highlights the significance of nanoparticles synthesized from photosynthesis in this context. Its purpose is to underscore the importance of sustainable farming practices. This approach is contrasted with conventional methods, elucidating the ecological and economic advantages of phyto-synthesized NPs.

This review discusses phyto-synthesized nanoparticles, including titanium dioxide, iron oxide, gold, silver, and copper. In addition, we review their ability to enhance crop growth and stress resistance. The primary focus is to elucidate the effects of phyto-synthesized NPs on plant development under drought stress. Noteworthy outcomes encompass improvements in seed germination, seedling growth, water absorption, photosynthesis, chlorophyll content, the activation of antioxidant defense mechanisms, and the modulation of hormonal responses. These results underscore the potential of phyto-synthesized NPs as agents for enhancing growth and mitigating stress. The review assesses the risks and challenges of using phyto-synthesized NPs in agriculture. Considerations include non-target organisms, soil, and environmental impacts. Further research is needed to determine the long-term effects, dangers, and benefits of phyto-synthesized NPs. Nanoparticles offer a targeted and sustainable approach for improving plant drought tolerance, outpacing traditional methods in ethics and ecological balance. Their mechanisms range from nutrient delivery to molecular regulation. However, the long-term environmental impact remains understudied. This review is critical for identifying research gaps and advancing sustainable agricultural practices amid global water scarcity.

Plants can be divided into two types, drought and flooding, both of which are very detrimental to plant growth. Among the various environmental stresses, drought is the most damaging to plants. Drought can reduce chlorophyll content Akbari *et al.* (2011) and cause stunted shoot growth but stimulate root growth (Navarro *et al.,* 2009). Fig. (14) The correlation between selenium and flooding stress in plants remains unclear to date. However, studies have demonstrated that Se can effectively alleviate drought stress in crops (Kaur *et al.,* 2014).

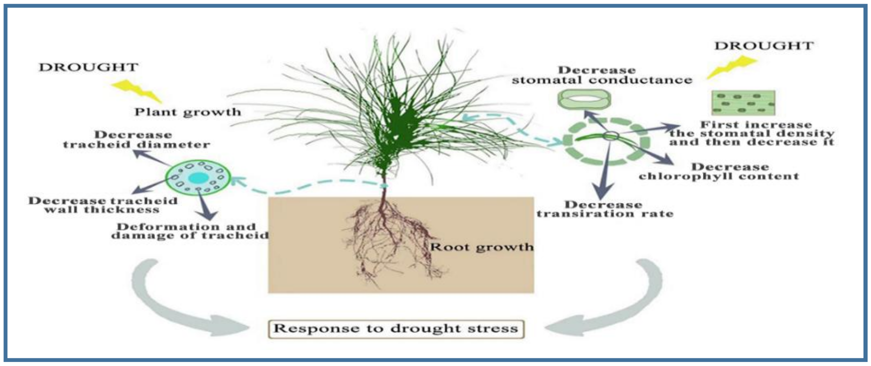


Fig.14: Ilustrates the Effects of drought stress on growth of P. sylvestris var. mongolica. After Meng *et al.,* (2023)

Meng *et al.* (2023) reported that the main purpose of this study was to study the changes in growth, root system, and tissue anatomical structure of Pinus sylvestris var. mongolica under soil drought conditions. In this study, the growth indexes and photosynthesis of P. sylvestris var. mongolica seedlings under soil drought stress were studied by pot cultivation. Continuous pot water control experiment of the indoor culture of P. sylvestris var. mongolica was carried out, ensuring that the soil water content of each treatment reached 80%, 40%, and 20% of the field moisture capacity as control, moderate drought and severe drought, respectively. The submicroscopic structures of the needles and roots were observed using a scanning electron microscope and a transmission electron microscope. The response of soil roots to drought stress was studied by root scanning. Moderate drought stress increased needle stomatal density, while under severe drought stress, stomatal density decreased. At the same time, the total number of root tips, total root length, root surface area, and root volume of seedlings decreased with the deepening of the drought. Furthermore, moderate drought and severe drought stress significantly reduced the chlorophyll a and chlorophyll b content in P. sylvestris var. mongolica seedlings compared to the control group. The needle cells were deformed and damaged, chloroplasts and mitochondria were damaged, gradually disintegrated, and the number of osmiophiles increased. There was also an increase in nuclear vacuolation.

The mechanism involved in this effect can be categorized into the following aspects. Selenium increases the activity of antioxidant enzymes in plants and improves the nonenzymatic breakdown of superoxide radicals Reynolds *et al.,* (2018), thereby reducing the accumulation of excess reactive oxygen species (ROS) and mitigating oxidative damage to cell membranes Fig. (15).

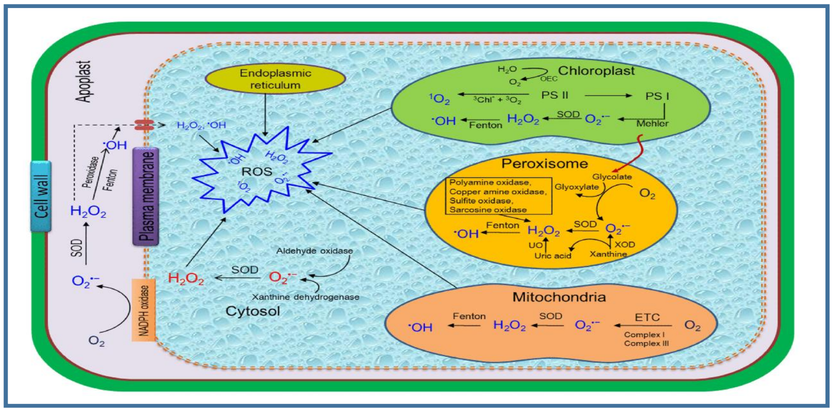


Fig 15: ROS generation process and localization in plant cells. In different cell organelles, ROS are produced through metabolic reactions where different enzymatic and non-enzymatic pathways are involved. (ROS) reactive oxygen species; ($H_2O_{2)}$ hydrogen peroxide; (1O^{-2} singlet oxygen; (ETC0 electron transport chain; (OH) hydroxyl radical; 3Chl) triplet chlorophyll; (PS I) photosystem I; (PS II) photosystem II; (O2) •− superoxide anion; (XOD) xanthine oxidase; (SOD) superoxide dismutase; (NADPH) nicotinamide adenine dinucleotide phosphate; (UO) urate oxidase. After Hasanuzzaman *et al.,* (2020, 2021).

ROS play important roles in plant resistance to abiotic stresses (Choudhury *et al.,* 2014). Plants subjected to drought produce large amounts of ROS, including superoxide anions, hydrogen peroxide, hydroxyl radicals, singlet oxygen, and methyl and lipid peroxide radicals (Renwei *et al.,* 2013) . The accumulation of ROS in plant cells can cause varying degrees of oxidative damage to biological membrane proteins and DNA and further disrupt the respiration and photosynthesis of plant cells (Nadarajah, 2020). Suitable concentrations of selenium can increase the activities of antioxidant enzymes or the contents of other antioxidant substances, thus accelerating the scavenging of intracellular free radicals (Andrade *et al.,* 2018). ROS elimination helps prevent oxidative stress and enhance the antioxidant capacity of plants. Cucumber seedlings grown in nutrient solution with 1 and 5 μmol L−1 have higher drought tolerance capacity than normal ones because the former have increased superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), and catalase (CAT) activities and reduced ROS accumulation in the root system (Jó´zwiak *et al.,* 2019).

Selenium also effectively reduces drought stress in olives. Spraying of olive leaves with 50 and 150 mg Se L^{-1} can significantly enhance the activities of APX, CAT, and glutathione peroxidase (GPOX) and the content of malondialdehyde (MDA), thus effectively scavenging excess ROS and protecting cells from oxidative damage (Proietti *et al.,* 2013). Selenium enhances water uptake and the relative water content in plants. Relative water content is an indicator of plant water status and reflects the balance between water availability and the transpiration rate of leaf tissues (Arndt *et al.,* 2015). The relative intracellular water content is significantly reduced when plants are under drought and inhibited nutrient uptake Wu *et al.,* (2018), which can lead to plant death in the long term. Exogenous Selenium can increase the relative water content of plant cells in crops, such as sorghum Aissa *et al.,* (2018), spring barley Habibi (2013), and canola Hemmati *et al.,* (2019), consequently reducing the stress-generated damage and improving the drought tolerance of plants. The underlying mechanism is that selenium promotes water uptake by the root system of plants under drought conditions. However, the details underlying the mechanism remain to be revealed.

The stimulation of chlorophyll and photosynthesis within plant cells using photosynthesized NPs has garnered significant attention in recent years due to its potential implications for environmental and agricultural sustainability. Photosynthesis is the fundamental process by which plants convert light energy into chemical energy, crucial for their growth and development. At the same time, carbon fixation plays a pivotal role in global ecosystems (Abasi *et al.,* 2022; Waadt *et al.,* 2022; Ebrahimi *et al.,* 2022; Mardi *et al.,* 2022). During environmental challenges like drought, plants often encounter reduced photosynthetic rates and chlorophyll degradation, leading to diminished growth and productivity.

However, research indicates that applying photosynthesized NPs can ameliorate these detrimental effects and enhance photosynthetic efficiency (Waadt *et al.,* 2022; Wahab *et al.,* 2022; Wahab *et al.,* 2023; Younas *et al.,* 2022; Ibrahim *et al.,* 2023). Moreover, phyto-synthesized NPs possess inherent antioxidant properties, which aid in combating the harmful impacts of reactive oxygen species (ROS) that accumulate during drought conditions. ROS can induce oxidative harm to cellular components, including photosynthetic pigments and chloroplasts. By neutralizing the effects of these harmful radicals, NPs can safeguard chlorophyll molecules from degradation and sustain optimal chlorophyll content within plant leaves (Samanta and Roychoudhury 2021; Noman *et al.,* 2021; Fouda *et al.,* 2022. Phyto-synthesized NPs have been found to modulate gene expression associated with photosynthesis, resulting in an upregulation of essential proteins and enzymes responsible for enhancing the photosynthetic rate. This molecular regulation improves photosynthetic efficiency even under adverse environmental conditions (Xiong *et al.,* 2021; Hasan *et al.,* 2022).

Phyto-synthesized NPs, such as ZnO-NPs, affect photosynthesis and chlorophyll levels differently. The outcomes may depend on nanoparticle concentration, size, and the particular plant species under investigation. As a result, further research is essential to elucidate the mechanisms of action of different NPs and their specific interactions with diverse plant systems, thereby enhancing their applications for promoting photosynthesis (Siddiqi and Husen, 2022; Khan *et al.,* 2021; Mardi *et al.,* 2022; García-Ovando *et al.,* 2022). Phyto-synthesized NPs can enhance plants' photosynthesis and chlorophyll content to enhance drought tolerance by optimizing the photosynthetic process and safeguarding chloroplasts against oxidative damage (Dimkpa *et al.,* 2012; Ali *et al.,* 2021; Noman *et al.,* 2021).
Selenium can possibly enhance the vigor of the root system to absorb water under drought conditions Fig. (16).

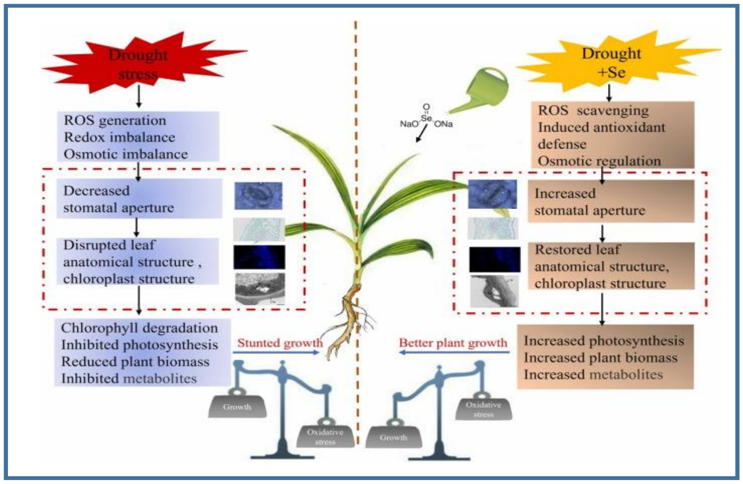


Fig. 16: Mechanism diagram of exogenous Se alleviating drought stress in G. macrophylla. After Yunyun *et al.,* (2024)

Selenium protects chlorophyll and maintains photosynthesis. Drought stress causes water deficiency in plants, closing of leaf stomata, and induction of stomatal conductance Ding *et al.,* (2020), which would further inhibit the supply of CO_2 and reduce the rate of CO_2 assimilation (Bao *et al.,* 2014). Therefore, long-term drought would eventually damage chlorophyll and prohibit photosynthesis in plants (Habibi, 2013). Selenium can effectively mitigate this damage to plants. Application of a 30 g/ha solution of Na_2SeO_4 to the leaves can significantly enhance stomatal conductance in spring barley cells under drought stress, thus enhancing photosynthesis (Habibi, 2013). Drought stress in rice can significantly reduce photosynthesis. Application of soil Se at a concentration of 0.5 mg kg^{-1} increases chlorophyll index, CO_2 assimilation efficiency, and net photosynthesis in rice (Arndt et al., 2015). Application of low concentrations of Na_2SeO_4 to canola under drought stress can significantly increase chlorophyll a and chlorophyll b contents, which enhance photosynthetic efficiency (Hemmati *et al.,* 2019).

This phenomenon may be ascribed to that Selenium can reduce the accumulation of ROS in plants subjected to drought (Renwei *et al.,* (2013). However, the exact mechanisms underlying this effect remains unclear. Interestingly, Zhou *et al.* (2018) found that flooded irrigation treatment increases the soil soluble Selenium concentration, and the Selenium in soil solution is present in the form of selenite and selenomethionine Selenium oxide. On the one hand, enhancement in the concentrations of soluble Selenium in the soil through flooding irrigation can significantly promote Selenium levels in grain and straw rice. On the other hand, Selenium at a relatively higher level is effective in mitigating the adverse effects of flooding in plants. Thus, irrigation practices and Selenium application can form a virtuous circle for plant growth.

4.2. Impact of selenium on plant under temperature stress

Temperature is important for plant growth. The biochemical reactions and physiological activities in plant cells are dependent on suitable temperature which is an important in abiotic stress for plant growth because it causes serious damage to plants, including dysregulation in photosynthetic processes, disturbance in enzyme activity, and metabolic disorders (Haghighi *et al.,* 2014; Du *et al.,* 2018) Fig.(17). Muhammad Ahmad *et al.* (2022) reported that Temperature is a significant parameter in agriculture since it controls seed germination and plant growth. Global warming has resulted in an irregular rise in temperature posing a serious threat to the agricultural production around the world. A slight increase in temperature acts as stress and exert an overall negative impact on different developmental stages including plant phenology, development, cellular activities, gene expression, anatomical features, the functional and structural orientation of leaves, twigs, roots, and shoots. These impacts ultimately decrease the biomass; affect reproductive process, decrease flowering, fruiting, and significant yield losses. Plants have inherent mechanisms to cope with different stressors including heat that may vary depending upon the type of plant species, duration and degree of the heat stress. Plants initially adapt avoidance and then tolerance strategies to combat heat stress. The tolerance pathway involves ion transporter, osmoprotectants, antioxidants, heat shock protein that help the plants to survive under heat stress.

To develop heat-tolerant plants using above-mentioned strategies requires a lot of time, expertise, and resources. On contrary, plant growth-promoting rhizobacteria (PGPRs) is a cost-effective, timesaving, and user-friendly approach to support and enhance agricultural production under a range of environmental conditions including stresses. PGPR produce and regulate various phytohormones, enzymes, and metabolites that help plant to maintain growth under heat stress. They form biofilm, decrease abscisic acid, stimulate root development, enhance heat shock proteins, deamination of ACC enzyme, and nutrient availability especially nitrogen and phosphorous. Despite extensive work done on plant heat stress tolerance in general, very few comprehensive reviews are available on the subject especially the role of microbes for plant heat tolerance.

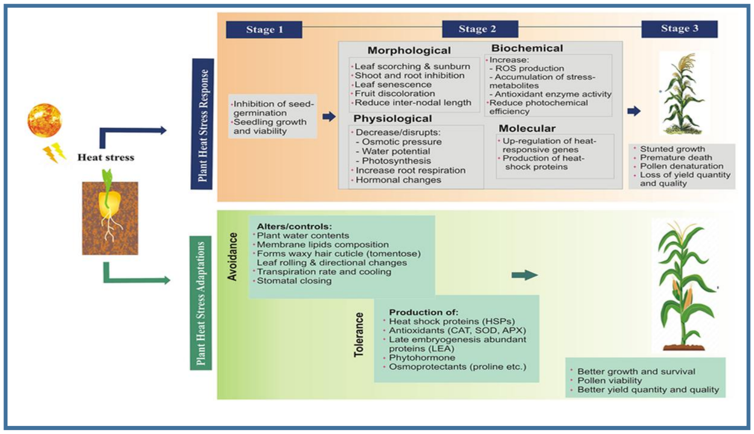


Fig. 17: Illustrates the heat stress responses and adaptation mechanisms in plants at different levels. After Muhammad Ahmad *et al.,* (2022)

They also summaries that global warming has become a critical challenge to food security, causing severe yield losses of major crops worldwide. Given the expanding needs for global food supply as well as the extreme pressure of population growth and climate change trajectories, strategies should primarily be focused on the right investigation on different abiotic stresses especially on heat stress that becomes a key problem in the last decade. Climate change and plant diseases is complex and challenging, as multiple aspects of plants, pathogens and the environment are involved. These factors include the distribution and abundance of taxa (geographical range, niche preference), their fitness and virulence, abiotic interactions, plant–microorganism evolutionary processes, host and vector biology, and environmental conditions. For instance, many soil opportunistic pathogens can cause disease outbreaks when environmental conditions become favourably for pathogen replication and vulnerable hosts are available (Cheng *et al.,* 2019; Trivedi *et al.,* 2022). Climate change can also indirectly affect plant–pathogen interactions through alterations in the biochemical, physiological, ecological and evolutionary processes of the plant host and/or pathogen (Velasquez et al., 2018; Cheng *et al.,* 2019; Desaint 2021; Trivedi *et al.,* 2022) (Fig. 18).

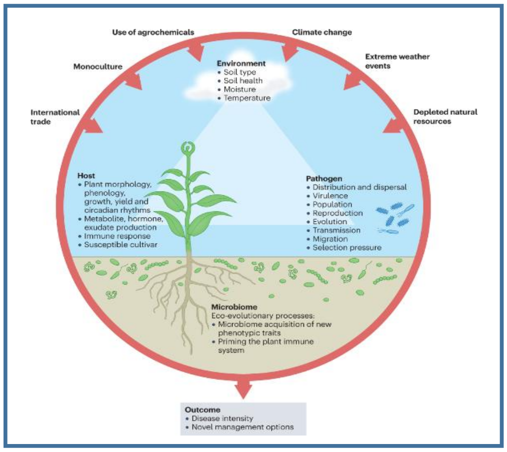


Fig. 18: Illustrates a new angle in the disease triangle paradigm that considers the plant microbiome as a pivotal factor influencing plant disease. After Brajesh *et al.,* (2023)

For example, prolonged drought causes water stress in forest trees, which results in increased susceptibility to infection by pathogens causing dieback disease from the genus Phytophthora, thus facilitating the occurrence of potentially new diseases (Desprez-Loustau *et al.,* 2006; Hossain *et al.,* 2019). Overall, the direct impacts of climate change are likely to vary depending on the pathogen, host identity and properties of biomes. Discussed in the following sections, there is limited but increasing evidence suggesting that climate change has a direct impact on pathogen virulence and disease development interactions among the plant, the environment, the soil and plant microbiome, and invading pathogens impact the outcome of infection processes, disease severity and productivity of the plant. Environmental change and human activities (for example, global commodity and climate change) drive pathogen evolution and have increased disease threats to global crops. Genetically uniform crop monocultures and high planting density in modern agriculture have accelerated the emergence of virulent pathogens capable of overcoming disease-resistant crop varieties and promote the pathogen's population size and genetic variability.

Similarly, overreliance on pesticides has also fostered rapid emergence of new strains of pathogens. Pathogen transmission and anthropogenic pathogen movement due to, for example, international trade spreads pathogens to places free of natural enemies, and allows exchange of genetic material via horizontal gene transfer, facilitating adaptation to local hosts. Depletion of natural resources and natural landscapes has caused deterioration of the agroecosystems diversity. Emerging evidence suggests that soil and plant microbiome influence the three angles of the disease paradigm the host, the pathogen and the environment by either facilitating or suppressing pathogen attacks, by affecting plant physiology and immune response, and providing a line of defence and manipulating environmental conditions. For example, in disease-suppressive soils, indigenous microbiome can reduce disease incidence, even in the presence of a pathogen, a susceptible host and a conductive environment. Explicit consideration of the role of the microbiome can improve our mechanistic understanding of disease outbreaks, which may lead to prediction that is more effective, monitoring and management of disease outbreaks. Better land management practices can improve overall soil health by influencing the diversity and functions of soil microbial communities, and could potentially be used to steer microbiome that suppress diseases.

Brajesh *et al.* (2023) reported that Plant disease outbreaks pose significant risks to global food security and environmental sustainability worldwide, and result in the loss of primary productivity and biodiversity that negatively influence the environmental and socio-economic conditions of affected regions. Climate change further increases outbreak risks by altering pathogen evolution and host–pathogen interactions and facilitating the emergence of new pathogenic strains. Pathogen range can shift, increasing the spread of plant diseases in new areas. In this Review, we examine how plant disease pressures are likely to change under future climate scenarios and how these changes will relate to plant productivity in natural and agricultural ecosystems. We explore current and future impacts of climate change on pathogen biogeography, disease incidence and severity, and their effects on natural ecosystems, agriculture and food production. We propose that amendment of the current conceptual framework, incorporation of eco-evolutionary theories into research could improve our mechanistic understanding, and prediction of pathogen spread in future climates, to mitigate the future risk of disease outbreaks. We highlight the need for a science–policy interface that works closely with relevant intergovernmental organizations to provide effective monitoring and management of plant disease under future climate scenarios, to ensure long-term food and nutrient security and sustainability of natural ecosystems.

The plants are more vulnerable to high temperatures because of their sessile nature. They exhibit physio-morphological, biochemical, and molecular adaptations against heat, but further investigations are required to understand the thermatolerance mechanism active in different plant species. The plants themselves produce antioxidants, reduce the stomatal conductance, activate heat responsive genes, and produce heat shock proteins, but on the other hand, exogenous or foliar application of chemicals like calcium chloride (CaCl2), salicylic acid, bio-stimulants, nanoparticles, and osmoprotectants are useful in sustainable agriculture. Furthermore, heat-sensitive genes can be targeted through CRISPR-Cas9 to develop heat-insensitive crops in the future. The heat resilient microbes produces phytohormones, ethylene, ACC deaminase, antioxidant enzymes, and HSP under heat stress enabling plants to maintain their growth under stress.

A recent review publishes the meta-analysis of 39 published studies in support of PGPR-mediated thermatolerance in plants. This supports that microbe-mediated solutions are more sustainable than developing heat-tolerant varieties as microbes are usually present in the soil and rhizosphere and can form associations with homologous as well as non-homologous hosts. So, a single heat resilient microbe-inoculum may be effective in more than one crop or plants. Furthermore, the microbes are multi-purpose and exhibit many other traits of plant interest apart from giving tolerance against heat stress making the microbe-therapy more effective than chemical or genetic engineering or breeding approaches. However, the molecular mechanisms involved in this tolerance may be studied in detail in different crops prone to heat stress. As plants cannot live in isolation in any environment, they have a direct impact of environment and interact with the microbes present in soil. Whereas microbes also interact with other microbes and to the environment. Therefore, this tri-partite association is very important for the stable functioning of the plants and microbes and over all agricultural sustainability in any given environment.

High-temperature stress causes premature leaf senescence, resulting in loss of chlorophyll, aggravation in membrane damage, and a decline in photosynthetic capacity (Chiang *et al.,* 2015) Figs. (19),(20).

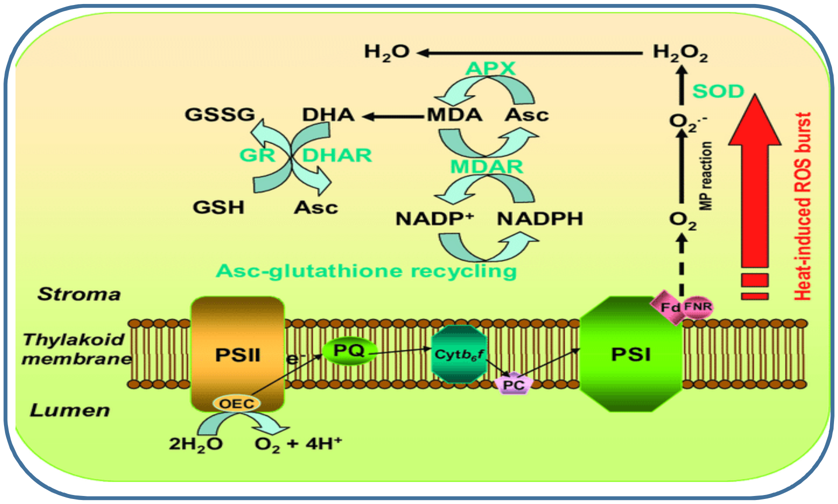


Fig. 19: Extensive and transient metabolic reprogramming in chloroplasts under heat stress. Major events of metabolic reprogramming in response to heat stress include chlorophyll breakdown, generation of reactive oxygen species (ROS), antioxidant defense, protein turnover, and metabolic alterations with carbon assimilation. With respect to the systemic acquired acclimation to heat stress in plants, diverse metabolic reprogramming in chloroplasts is required for optimizing plant growth and development during high temperature stresses. After Wang *et al.,* (2018)

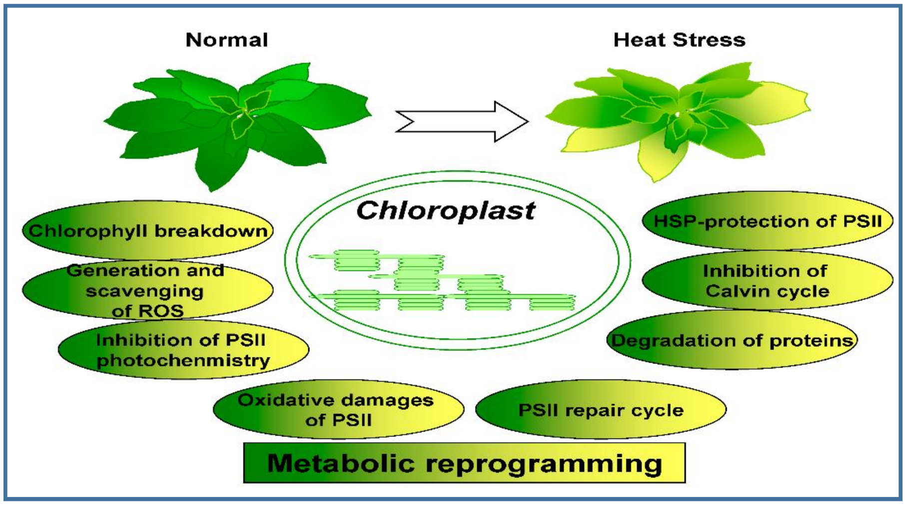


Fig. 20: Representative scheme of reactive oxygen species (ROS) generation and scavenging in chloroplasts under heat stress. High temperature stress triggers oxidative bursts of superoxide and/or hydrogen peroxide in plants. The transfer of excitation energy in the photosystem II (PSII) antenna complex and the electron transport in the PSII reaction center can be inhibited by heat stress. It has been established that ROS are generated on both the electron acceptor and the electron donor side of PSII under heat stress during which electron transport from the manganese complex to plastoquinone (PQ) is limited. The leakage of electrons to molecular oxygen on the electron acceptor side of PSII forms O2 •−, inducing initiation of a cascade reaction leading to the formation of H2O2. A diversified ROS-scavenging network functions in concert in chloroplasts, mainly including antioxidants and APX-glutathione cycle, to keep the equilibrium between ROS production and scavenging. The efficient enzymatic scavenging systems are composed of several key enzymes, including superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione peroxidase (GPX) and glutathione-S-transferase (GST) and non-enzymatic systems contain antioxidants such as ascorbic acid (Asc) and glutathione (GSH). After Wang *et al.,* (2018)

Low-temperature stress inhibits chlorophyll biosynthesis and antioxidant enzyme activity but increases ROS production and cell membrane damage (Liu *et al.,* 2018; Lunn *et al.,* 2022). Therefore, high and low temperatures can restrain plant growth, even leading to plant death in severe cases. Selenium can effectively regulate high or low-temperature stress in plants. This effect is attributed to the following mechanisms. High-temperature stress accelerates the degradation of chlorophyll Park *et al.,* (2009), increases photorespiration, reduces ribulose-1, 5-bisphosphate carboxylase/oxygenase (RuBisCO) activity, and interferes with the electron transport chain of the photosynthetic system in plants (Mathur *et al.,* 2018).

Selenium can protect chlorophyll and mitigate temperature stress-induced damage to photosynthesis Iqbal *et al.,* (2015). Seliem *et al.,* (2020) found that Selenium can protect chlorophyll and mitigate temperature stress-induced damage to photosynthesis Iqbal *et al.,* (2015). Wheat seeds soaked with 26.45 µmol L^{-1} sodium selenate and germinated at a low temperature (3 or 5 ◦C) show enhanced CAT and polyphenol oxidase activities and reduced ROS concentration Akladious (2012) , thus protecting the cell membrane. Wheat seedlings treated with Selenium under low-temperature stress also significantly enhance the activities of POD and APX (Abbas, 2012) Fig. (21).

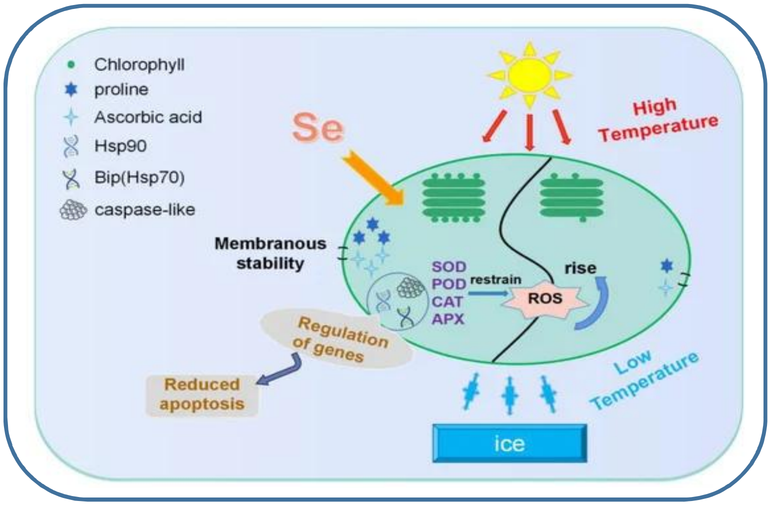


Fig. 21: Illustrates the patterns of Se mitigating temperature stress in plants. The ellipse indicates plant leaf cells under high and low-temperature stress, the left half indicates cells treated with Se. After Liu *et al.,* (2022)

Liu *et al.* (2022) stated that plant growth is affected by various abiotic stresses, including water, temperature, light, salt, and heavy metals. Selenium is not an essential nutrient for plants but plays important roles in alleviating the abiotic stresses suffered by plants. This article summarizes the Selenium uptake and metabolic processes in plants and the functions of Selenium in response to water, temperature, light, salt, and heavy metal stresses in plants. Selenium promotes the uptake of beneficial substances, maintains the stability of plasma membranes, and enhances the activity of various antioxidant enzymes, thus alleviating adverse effects in plants under abiotic stresses.

A low concentration of sodium selenite solution (28.90 µmol L^{-1}) significantly increases the activities of SOD, CAT, and POD in strawberry seedlings under low-temperature stress, which effectively alleviate oxidative damage in strawberry seedlings (Huang *et al.,* 2018). In cotton under high-temperature stress (35/22°C, day/night), Selenium can protect chlorophyll and mitigate temperature stress-induced damage to photosynthesis (Iqbal *et al.,* 2015) Fig. (22).

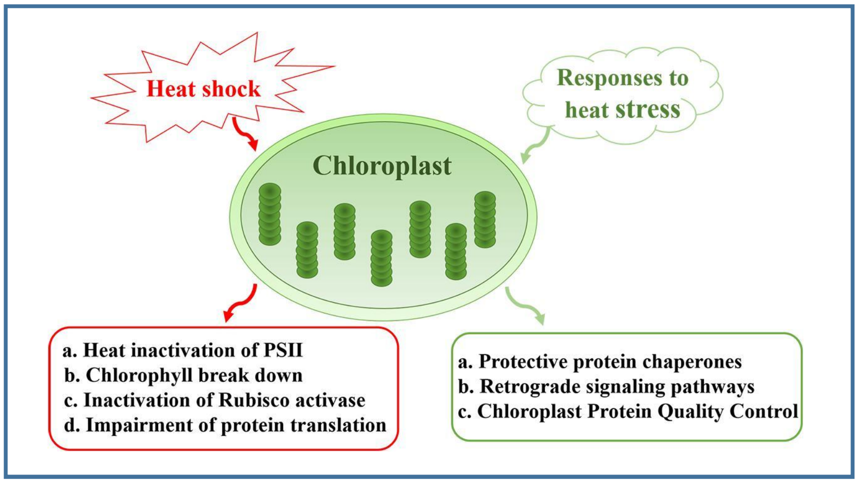


Fig. 22: Sensitivity and responses of chloroplasts under heat stress. Major effects of heat stress on chloroplasts include heat inactivation of PSII, Chl breakdown, inactivation of Rubisco, and impairment of protein translation. In response to heat stress, chloroplasts generate a large number of protein chaperones to protect PSII. Meanwhile, chloroplast protein quality control plays a role in maintaining proteostasis under conditions of environmental stress. Chloroplasts also participate in retrograde signal pathways that protect cellular integrity and the normal growth of plants. After Hu *et al.,* (2020)

Hu *et al.* (2020) reported that increasing temperatures caused by global warming threaten agricultural production, as warmer conditions can inhibit plant growth and development or even destroy crops in extreme circumstances. Extensive research over the past several decades has revealed that chloroplasts, the photosynthetic organelles of plants, are highly sensitive to heat stress, which affects a variety of photosynthetic processes including chlorophyll biosynthesis, photochemical reactions, electron transport, and CO_2 assimilation. Important mechanisms by which plant cells respond to heat stress to protect these photosynthetic organelles have been identified and analyzed. Studies that are more recent have made it clear that chloroplasts play an important role in inducing the expression of nuclear heat-response genes during the heat stress response. In this review, we summarize these important advances in plant-based research and discuss how the sensitivity, responses, and signaling roles of chloroplasts contribute to plant heat sensitivity and tolerance.

4.3. Selenium enhances osmotic protection in plants.

Proline and soluble sugars act as osmotic protectants and regulate cellular metabolic activities (Ozturk *et al.,* 2021) Fig. (23).

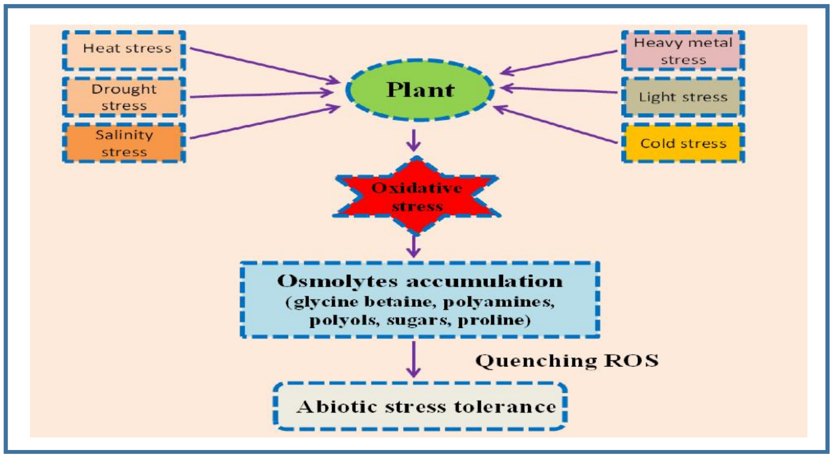


Fig. 23: Schematic representation of plants response to various abiotic stresses and the role of osmolytes to counteract reactive oxygen species under stressful conditions. After Sharma *et al.,* (2019)

Sharma *et al.* (2019) stated that plants face a variety of abiotic stresses, which generate reactive oxygen species (ROS), and ultimately obstruct normal growth and development of plants. To prevent cellular damage caused by oxidative stress, plants accumulate certain compatible solutes known as osmolytes to safeguard the cellular machinery. The most common osmolytes that play crucial role in osmoregulation are proline, glycine-betaine, polyamines, and sugars. These compounds stabilize the osmotic differences between surroundings of cell and the cytosol. Besides, they also protect the plant cells from oxidative stress by inhibiting the production of harmful ROS like hydroxyl ions, superoxide ions, hydrogen peroxide, and other free radicals. The accumulation of osmolytes is further modulated by phytohormones like abscisic acid, brassinosteroids, cytokinins, ethylene, jasmonates, and salicylic acid. It is thus important to understand the mechanisms regulating the phytohormone-mediated accumulation of osmolytes in plants during abiotic stresses. In this review, we have discussed the underlying mechanisms of phytohormone-regulated osmolyte accumulation along with their various functions in plants under stress conditions. A high level of free proline is one of the factors enhancing cold tolerance in plants under low-temperature stress (Kavi Kishor *et al.,* 2014). Soluble sugars act as osmotic protectants and important metabolic substrates and play a dynamic role in controlling numerous procedures in plant development (Chen *et al.,* 2020).

Selenium can increase proline content in plants possibly by affecting the activities of proline synthesis-related enzymes (Iqbal *et al.,* 2015; Hawrylak-Nowak *et al.,* 2010). Sorghum seeds exposed to low concentrations of selenate (15.87 and 31.75 µmol L^{-1}) show a significant increase in proline and soluble sugar contents when germinated under low temperatures (4 ◦C or 8 ◦C) (Abbas 2012) . Similar phenomena were observed in potatoes and cucumber. Spraying 126.6 µmol L^{-1} SeNPs on the leaves of

Coriandrum sativum can significantly increase it soluble sugar content by 1.5 times (Sardar *et al.,* 2022). These studies suggest that appropriate concentrations of Selenium effectively increase the accumulation of proline and soluble sugar and enhance cold resistance in plants under low-temperature stress.

4.4. Selenium regulates the expression of genes associated under temperature stress.

Tobacco cell cultures treated with selenate show lower expression levels of some stress-related protein genes, such as the heat-stimulated protein Hsp90, BiP (Hsp70 family), 14-3-3s, and cytochrome c, when they are under high-temperature stress (5 min, 50 ◦C). HSP90 and HSP70 function in organelle-specific protein sorting Malerba and Cerana (2018), Hahn *et al.,* (2011) and ubiquitin-mediated proteasomal degradation Hafrén *et al.,* (2010) and are related to thermal resistance in plants Sangster and Queitsch (2005). Therefore, the regulation of these genes by Selenium regulates the expression of genes associated under temperature stress would contribute to protect plants from heat stress.

4.5. Impacts of selenium under light stress

Light is the only source of energy for compound accumulation and plays an important role in plant growth, physiology, biochemistry, and morphological establishment in plants Gallé *et al.,* (2019). Plants cannot photosynthesize adequately under low light, leading to a deficiency in energy and inhibiting their growth (Miotto, *et al.,* 2021) Fig (24).

Strong light can damage the chloroplasts and weaken photosynthesis (Pan and Guo, 2016). Studies have demonstrated that low concentrations of Se can protect cystoid membranes, maintain the stability of cystoids and chloroplast stroma, significantly increase the content of beneficial elements directly related to the structural function of chloroplasts in plant leaves, and aid in the recovery of membrane structure under low or strong light stress (Malerba and Cerana, 2018; Shanker, 2006). Selenium alleviates chloroplast damage by regulating antioxidant substances when plants are exposed to strong and low light. Potato plants exposed to 600 mmol m^{-2} s^{-1} of strong light show remarkable alteration in transcriptive levels of chloroplast CuZnSOD and GPX when they are treated with low concentrations of Se (Seppänen *et al.,* 2003).

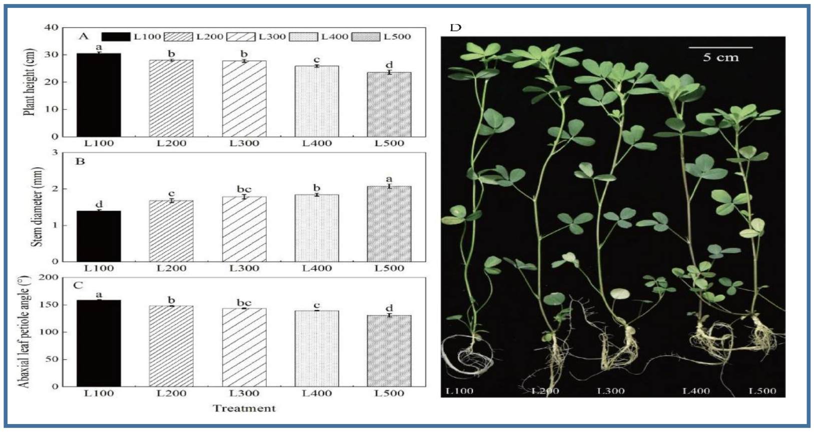


Fig. 24: Illustrates the changes in phenotype and plant traits of alfalfa as affected by light treatments. The plant height (A), stem diameter (B), abaxial leaf petiole angle (C) and plant phenotype (D) of alfalfa plants under different light intensity treatments. L100, L200, L300, L400 and L500 refer 100, 200, 300, 400 and 500 µmol m^{-2} s^{-1}, respectively. Vertical bars indicate 1 s.e. of the mean (n = 4). D Figure 1. Changes in phenotype and plant traits of alfalfa as affected by light treatments. The plant height (A), stem diameter (B), abaxial leaf petiole angle (C) and plant phenotype (D) of alfalfa plants under different light intensity treatments. L100, L200, L300, L400 and L500 refer 100, 200, 300, 400 and 500 µmol m^{-2} s^{-1}, respectively. Vertical bars indicate 1 s.e. of the mean (n = 4). Different lowercase letters on the different bar mean significant differences ($p < 0.05$). After Tang *et al.,* (2022)

Tang *et al.* (2022) reported that to understand how light intensity influences plant morphology and photosynthesis in the forage crop alfalfa (*Medicago sativa* L. cv. Zhongmu 1), we investigated changes in leaf angle orientation, chlorophyll fluorescence, parameters of photosynthesis and expression of genes related to enzymes involved in photosynthesis, the Calvin cycle and carbon metabolism in alfalfa seedlings exposed to five light intensities (100, 200, 300, 400 and 500 μmol m^{-2} s^{-1}) under hydroponic conditions. Seedlings grown under low light intensities had significantly increased plant height, leaf hyponasty; specific leaf area, photosynthetic pigments, leaf nitrogen content and maximal PSII quantum yield, but the increased light-capturing capacity generated a carbon resource cost (e.g., decreased carbohydrates and biomass accumulation). Increased light intensity significantly improved leaf orientation toward the sun and upregulated the genes for Calvin cycle enzymes, thereby increasing photosynthetic capacity. Furthermore, high light (400 and 500 μmol m^{-2} s^{-1}) significantly enhanced carbohydrate accumulation, accompanied by gene upregulation and increased activity of sucrose and starch-synthesis-related enzymes and those involved in carbon metabolism. Together, these results advance our understanding of morphological and physiological regulation in shade avoidance in alfalfa, which would guide the sidentification of suitable spatial planting patterns in the agricultural system

This result suggests that Selenium facilitates the activation of protection mechanisms when plants are exposed to intense light. Elevation in the response to oxidative stress induced by Selenium enhances the stability of photosynthetic pigments and promotes the recovery of chlorophyll in plants after light stress, even making the chlorophyll content reach the initial level in plants before light stress (Ahmad *et al.,* 2016) Fig.(25).

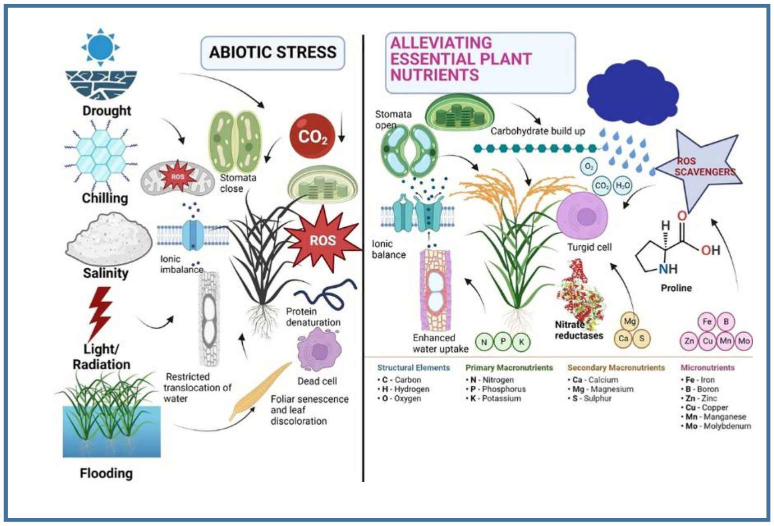


Fig. 25: Negative impacts of abiotic stress and their alleviation using plant nutrients in plant After Swain *et al.,* (2023)

Ultraviolet (UV) light is another form of light stress aside from low or strong light. Recent studies have highlighted UV as a regulator of plant growth and development rather than as a destructive stressor (Björn, 2015). High UV intensity can decrease photosynthetic pigment levels, respiratory potential, Ca^+ concentration, and leaf thickness (Yao *et al.,* 2010) Fig. (26). Swain *et al.* (2023) stated that plant body is a complex of several biomolecules, among them phytohormones are the molecules produced in very low concentrations, however, they show their active participation in regulatory activities (Shabir *et al.,* 2016). The cellular activities are mostly regulated by the chemical communication inside the plant body with low-volume phytohormones (Vob *et al.,* 2014). Phytohormones are most important to regulate various signal transduction pathways during abiotic-stress response. They regulate external as well as internal stimuli (Kazan, 2015). Auxin, cytokinin (CK), gibberellic acid (GA), ethylene, abscisic acid, brassinosteroids, salicylic acid, jasmonates, and Strigolactones are the major phytohormones that have the major network in plant growth and development as well as in alleviating abiotic stress in plants.

Nutrients are another crucial component that can minimize the effect of abiotic stress in plants by maintaining the inner homeostasis of the cell. Plant nutrients are considered the available form of food for plants for their normal growth and development. The plant nutrients are grouped into primary nutrients like nitrogen (N), phosphorus (P), and potash (K); secondary nutrients like calcium (Ca), magnesium (Mg)and sulfur (S); micronutrients like boron(B), zinc (Zn), iron (Fe)conditions, copper

(Cu); and other beneficial nutrients like cobalt (Co), selenium (Se), silicon (Si). Due to global climate change, plant suffers a lot from nutrient deficiency. It was also noted that nutrient deficiencies are the major cause of yield loss during abiotic stress. Hence, proper nutrient management can elevate abiotic stress conditions in plants to some extent. Plant nutrients can mitigate stress also by activating stress resistance genes, enhancing antioxidant enzyme activity, creating osmoprotectants in cells, synthesizing heat shock proteins and other proteins related to stress tolerance, decreasing ROS activities, creating membrane stability, repairing DNA, enhancing chlorophyll content in leaves, reducing the uptake of heavy metals in the plant.

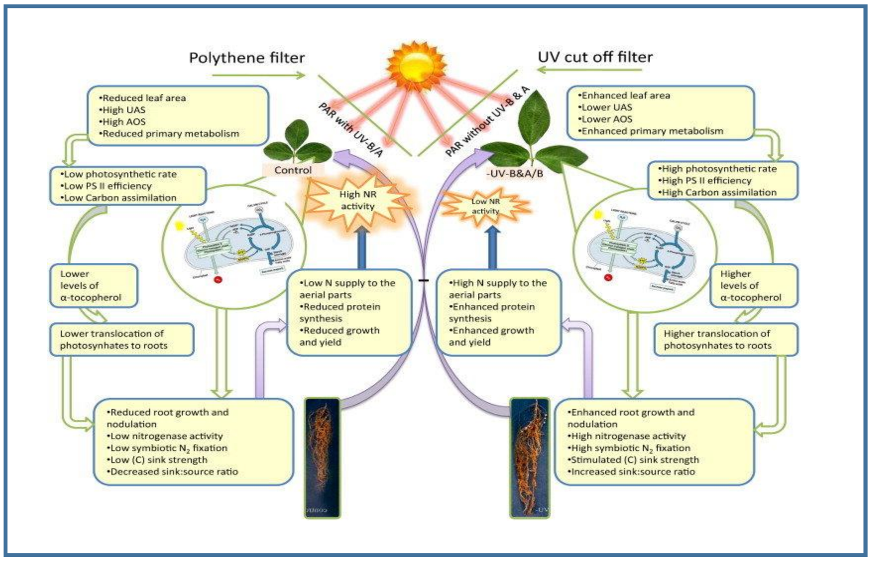


Fig. 26: Illustrates the impact of UV radiation on photosynthesis, UAS, α-tocopherol, leghemoglobin, nodulation, NRA and growth in soybean plants. After Baroniya *et al.,* (2014)

Baroniya *et al.* (2014) reported that a field experiment was conducted to study the impact of the exclusion of the solar UV components on growth, photosynthesis and nitrogen metabolism in soybean (Glycine max) varieties PK-472, Pusa-24, JS 71-05, JS-335, NRC-7 and Kalitur. The plants were grown in specially designed UV exclusion chambers wrapped with filters to exclude UV-B or UV-A/B and transmitted all UV. Exclusion of UV significantly enhanced the growth of the aerial parts as well as the growth of the below ground parts in all of the six soybean varieties. Nitrate reductase activity (NRA) was significantly reduced, whereas leghemoglobin (Lb) content, total soluble protein, net photosynthesis (Pn) and α-tocopherol content were enhanced after UV exclusion. The exclusion of solar UV-A/B enhanced all parameters largely than the exclusion of solar UV-B in four of the six varieties of soybean except for NRC-7 and Kalitur. These two varieties responded more to UV-B exclusion compared to UV-A/B exclusion. A significant inverse correlation between the NRA and the number of nodules per plant was observed. The extent of response in all parameters was greater in PK-472 and JS71-05 than that in Kalitur and JS-335 after UV exclusion. The exclusion of UV augmented the growth of nodules, Lb content and α-tocopherol levels and conferred higher rates of Pn to support better growth of nodules. Control plants (+UV-A/B) seemed to fulfill their N demand through the assimilation of NO^{-3} resulting in lower symbiotic nitrogen fixation and higher NR activity.

Selenium effectively mitigates the effects of UV radiation on plants. Pumpkin plants grown in the field are sensitive to UV-B radiation. UV-B negatively affects the electron flow at the end of the electron transport system and impairs the flow of electrons in the respiratory chain, thus decreasing the yield (Germ *et al.,* 2005). Foliar spraying of Selenium counteracts this effect; significantly increasing the fruit yield of plants exposed to UV-B radiation (Germ *et al.,* 2005). However, the underlying mechanism remains unclear. Evidence suggests that Selenium can enhance the accumulation of antioxidant substances, increase the activity of antioxidant enzymes, and reduce the accumulation of ROS in plants under UV stress. Wheatgrasses germinated from Selenium -rich wheat grains exhibit increased total flavonoid and phenolic contents than non-seleniferous ones when they are exposed to UV-B stress (Jaiswal *et al.,* 2018). The former also shows a higher scavenging rate of DPPH radicals and activities of SOD and CAT but lower lipid peroxidation (Jaiswal *et al.,* 2018). Treatment with Na_2SeO_3 solutions (28.90, 57.80, and 115.6 μmol L^{-1}) also increases the isoflavone content and inhibition of NO production in soybean under UV stress (Mata-Ramírez *et al.,* 2019). The antioxidant activity of soybean cells is thus increased. Aside from increasing antioxidant capacity, Selenium can promote the accumulation of UV-absorbing compounds. Golob *et al.* (2017) found that foliar spraying with 52.91 μmol L^{-1} sodium selenate significantly increases the content of some UV-absorbing compounds, such as Si and Ca, in wheat seedlings under UV radiation (Klanˇcnik *et al.,* 2014). It can also increase light reflectance and reduce transmittance, thus enhancing the protection of wheat under UV stress (Golob *et al.,* 2017).

4.6. Impacts of selenium on salt stress

High salt levels in the soil cause salt stress in plants. Salt stress can induce nutritional imbalance, water deficit, oxidative stress, and disruption of cellular ion homeostasis in plants (Tester and Tester, 2008). Plants can be generally classified into two major types according to salinity tolerance, namely, halophytes (salt-tolerant) and glycophytes (salt-sensitive). Glycophytic plants can tolerate relatively low salt concentrations ranging from 50 mM to 250 mM NaCl, whereas halophytic plants are adapted to natural conditions of high salt (approximately 500–1000 mM NaCl) in the soil (Vicente *et al.,* 2004). The Food and Agriculture Organization of the United Nations states that salt stress poses a serious threat to more than 6% of the land (Parihar *et al.,* 2014). Salt stress reduces the uptake of water and nutrients, increases the osmotic potential of plant cells Hanin *et al.,* (2016), inhibits plant photosynthesis, and alters plant metabolism and physiology, thereby inhibiting plant growth and reducing yields (Abdelrahman *et al.,* 2018). For instance, when Na+ and Cl- are taken up in large quantities by the root system, metabolic impairment and photosynthetic efficiency reduction would occur (Mäser *et al.,* 2002; Tester and Tester, 2008). Selenium can enhance resistance to salt stress and mitigate the negative effects of salinity in plants. The underlying mechanisms are concluded as follows Fig. (27).

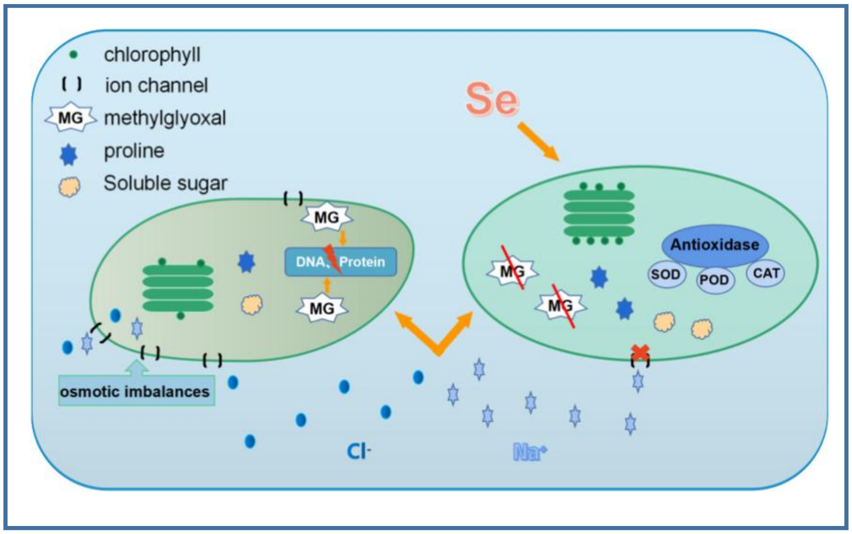
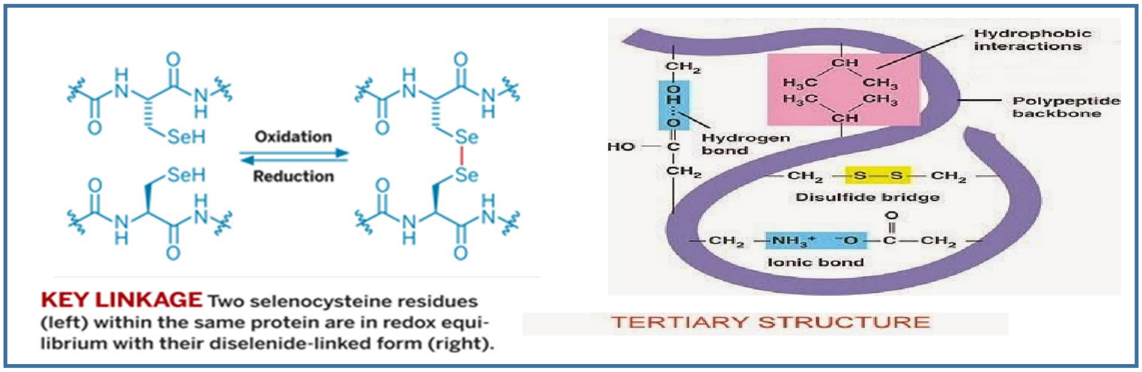


Fig. 27: Illustrates Patterns of Selenium mitigating salt stress in plants. The left shows plant cells under Na + salt stress. The right shows a cell treated with Selenium under salt stress. After Liu *et al.,* (2023).

Liu *et al.* (2023) reported that plant growth is affected by various abiotic stresses, including water, temperature, light, salt, and heavy metals. Selenium is not an essential nutrient for plants but plays important roles in alleviating the abiotic stresses suffered by plants. This article summarizes the Selenium uptake and met- abolic processes in plants and the functions of Selenium in response to water, temperature, light, salt, and heavy metal stresses in plants. Selenium promotes the uptake of beneficial substances, maintains the stability of plasma membranes, and enhances the activity of various antioxidant enzymes, thus alleviating adverse effects in plants under abiotic stresses. Future research directions on the relationship between Selenium and abiotic stresses in plants are proposed. This article will further deepen our under- standing of the relationship between Selenium and plants.

4.7. Selenium enhances photosynthesis.

Selenium is effective in enhancing chlorophyll fluorescence parameters and photosynthetic pigment content and maintaining the ultrastructure of chloroplasts in plants under salt stress (Liang *et al.,* 2020; Hawrylak-Nowak 2009). Diao *et al.* (2014) found that Selenium could promote net photosynthetic rate and stomatal limitation and reduce intercellular CO_2 concentration, thus promoting the photosynthesis of tomato seedlings under salt stress. Enhancement of photosynthesis may be because the chloroplast membrane system of leaf cells is less damaged and maintains better integrity by Selenium in plants under salt stress (Kong *et al.,* 2005). However, Selenium concentration must be set carefully because Selenium accumulated in high amounts in the leaves may inhibit the enzymatic kinetics or electron transport chain in photosynthesis (Liang *et al.,* 2020; Zhang *et al.,* 2018; Sui *et al.,* 2018). The tertiary structure of most proteins depends on the formation of disulfide bonds (S-S). A new diselenide bond (Se-Se) or selenosulfide bond (Se-S) can easily form because of the replacement of Cys by SeCys in proteins when the plant cells contain a high concentration of Selenium (Liang *et al.,* 2020) Fig. (28).



KEY LINKAGE Two selenocysteine residues (left) within the same protein are in redox equilibrium with their diselenide-linked form (right).

Fig. 28: Illustrates the tertiary structure of most proteins depends on the formation of disulfide bonds (S-S) or selenosulfide bond (Se-S) can easily form because of the replacement of Cys by SeCys in proteins when the plant cells contain a high concentration of Selenium.

This phenomenon disrupts the structure of the PSII complex in chloroplasts and exerts a strong inhibitory effect on photosynthetic electron transfer (Liang *et al.,* 2020). In addition, the substitution of Selenium for sulfur in the key enzymes involved in chlorophyll synthesis reduces their activity, disrupts the biochemical reaction, and severely hampers chlorophyll synthesis (Liang *et al.,* 2020). Selenium regulates osmotic pressure and maintains the stability of the plasma membrane in plants under salt stress. Selenium can increase the content of relevant osmotic protectants, such as proline, soluble sugars, and soluble proteins, and alleviate electrolyte leakage from the cell membranes in plants under salt stress (Elkelish *et al.,* 2019). Selenium also reduces the content of the lipid peroxidation product MDA and helps maintain membrane stability. For example, free proline content is increased by 72.7% and Metal (202DA content is reduced by 87.5% in NaCl-stressed wheat leaves treated with a low concentration (1–8 µmol L^{-1}) of Na_2SeO_3.

This treatment can also minimize electrolyte leakage from plant cell membranes by approximately 58% compared with the control group (Liang *et al.,* 2020). Selenium enhances antioxidant enzyme activity and alleviates oxidative damage. Selenium effectively enhances the activities of antioxidant enzymes (e.g., SOD, POD, APX, CAT), thus scavenging excess ROS and free radicals in the body and alleviating the oxidative stress damage caused by salt stress in plants. The enhancement of antioxidant enzyme activities and alleviation of oxidative stress in plants exposed to salt stress by Selenium have been reported in many species, such as wheat Liang *et al.,* (2020), bitter melon Sheikhalipour *et al.,* (2021) soybean Rahman *et al.,* (2021), melon Keling *et al.,* (2013), and peanut Hussein *et al.,* (2019). In melon plants, salt stress increases electrolyte leakage and MDA content. Treatment with Selenium can significantly reduce the symptoms of salt stress by significantly increasing the activities of SOD, POD, and CAT by 130%, 50%, and 20%, respectively, when compared with non-seleniferous melon plants, thus reducing the oxidative damage of ROS (Keling *et al.,* 2013).

Selenium enhances the glyoxalase system to protect biomolecules, such as nucleic acids and proteins. Plants under salt stress accumulate excess methylglyoxal, which subsequently produces carbonyl stress, damaging the biomolecular proteins, DNA, RNA, lipids, and biofilms. The glyoxalase system in plants can effectively remove excess methylglyoxal while regulating GSH regeneration to maintain the dynamic balance in cells Mostofa *et al.,* (2018), Handa Rahman *et al.,* (2021) found that Selenium treatment enhances the antioxidant defense and glyoxalase systems of soybean under salt stress, thus protecting lipids, nucleic acids, proteins, and other biomolecules (Elkelish *et al.,* 2019; Sheikhalipour *et al.,* 2021). Selenium is effective in reducing Na+ uptake and accumulation in plants under NaCl stress. Increased salt concentrations in the soil decrease the ability of plants to take up water (Germ *et al.,* 2005). Once Na^+ and Cl^- are taken up in enormous amounts by the roots, the metabolic processes would be impaired, and the photosynthetic efficiency would be decreased (Yao *et al.,* 2010; Wu *et al.,* 2019; Rodríguez-Ortega, *et al.,* 2019). Sheikhalipour *et al.* (2021) applied chitosan SeNPs to bitter melon under NaCl stress and found that this treatment increases the uptake of K^+ but reduces the uptake of Na^+, thus improving salt tolerance in bitter melon (Jiang *et al.,* 2017; Jawad *et al.,* 2020).

4.8. Impacts of selenium on heavy metal stress

Heavy metals include Cd, Hg, Pb, Cu, and Cr, which are introduced into the ecosystem due to mining, chemical, and agricultural production activities. Heavy metals induce lipid peroxidation. The balance between the production and scavenging of free radicals in cells is disrupted when plants take up excessive amounts of heavy metals, resulting in the accumulation of large amounts of ROS, which further trigger the peroxidation of unsaturated fatty acids in membranes and damage membrane structure and function (Shahid *et al.,* 2014). High concentrations of these elements not only cause poisoning in plants but also endanger the health of animals that consume them, eventually posing a risk to human health (Khanam *et al.,* 2020). The studies concerning the correlation between Selenium and heavy metals and conclude the mechanism involved in the mitigation effects of Selenium on heavy metal stress in plants Fig. (29)

Yuan *et al.* (2024) reported that human activities, such as mining, industrialization, industrial waste emissions, and agricultural practices, have caused heavy metals to become widespread and excessively accumulated in soil. The high concentrations of heavy metals in soil can be toxic to plants, severely affecting crop yield and quality. Moreover, these heavy metals can also enter the food chain, affecting animals and humans and leading to various serious illnesses. Selenium is not only an essential element for animals and humans but is also beneficial for plants, as it promotes their ability to respond actively to biotic and abiotic stresses. The global issue of Selenium deficiency in diets has made plants the primary source for human Selenium supplementation.

This paper comprehensively reviews the effects of heavy metal stress on plant growth and development, physiological responses of plants to such stress, and the intracellular transport processes of heavy metals within plants. It particularly focuses on the mechanisms by which Se alleviates heavy metal stress in plants. Additionally, the study delves into how Selenium significantly enhances plant tolerance mechanisms against typical heavy metals, such as cadmium (Cd), lead (Pb), and mercury (Hg). This integrative research not only expands the boundaries of research in the field of plant heavy metal stress and Selenium application but also provides new perspectives and solutions for understanding and addressing complex environmental heavy metal pollution issues. By integrating these aspects, this paper not only fills existing gaps in the literature but also offers comprehensive scientific basis and strategic recommendations for environmental protection and sustainable agriculture development.

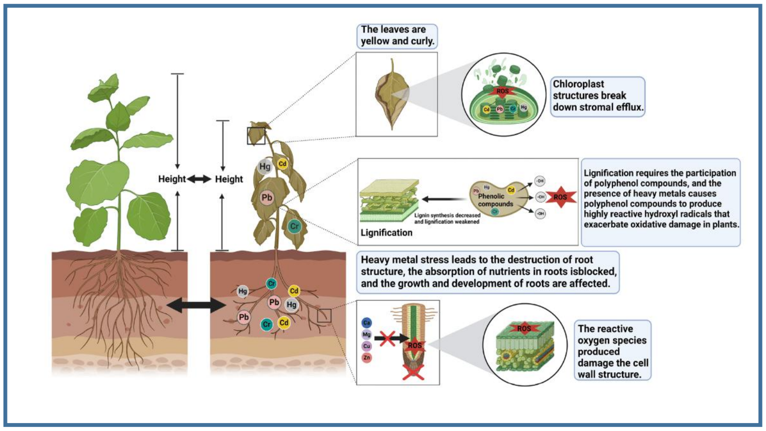


Fig. 29: Illustrates the effects of heavy metal stress on plant growth. After Yuan *et al.,* (2024)

Selenium enhances plant photosynthesis. Heavy metal toxicity can inhibit photosynthesis by triggering the degradation of chlorophyll molecules by enhancing chlorophyllase activity and replacing the central Mg^+ in the porphyrin ring, affecting overall plant growth and yield (Sitko *et al.,* 2021). However, Selenium significantly enhances chlorophyll a, chlorophyll b, and total chlorophyll contents in plants under heavy metal stress, thereby facilitating photosynthesis (Sardar *et al.,* 2022; Tran *et al.,* 2021). Selenium also helps rebuild damaged cell membranes, chloroplast structures, and photosynthetic system components in plants (Kong *et al.,* 2005; Ismael *et al.,* 2019; Filek *et al.,* 2010). Selenium enhances transpiration in plants. The water potential, leaf osmotic potential, and relative water content are significantly reduced in plants under heavy metal stress Sardar *et al.,* (2022), because ion channels and stomata of cell membranes are damaged or even closed, resulting in the reduced transpiration and disruption of plant growth and metabolism (Keyster *et al.,* 2020) .

Selenium can enhance transpiration and water transport in plants under heavy metal stress and reduce leaf temperature. SeNPs (126.6 µmol L^{-1}) effectively improves the water potential (80%), leaf osmotic potential (52%), gas exchange properties, and transpiration rate of C. sativum (Sardar *et al.,* 2022). Selenium enhances osmotic protection. It can enhance the proline and soluble sugar contents and help maintain the stability of the plasma membrane in plants under heavy metal stress (Sardar *et al.,* 2022). Proline enhances membrane stability and reduces the degradation of proteins and carbohydrates (Zhang *et al.,* 2016). Soluble sugars are important osmotic protectants for plants (Afzal *et al.,* 2021). Application of low concentrations of SeNPs (126.6 µmol L−1) effectively enhances the proline content and total soluble sugar content of C. sativum under Cd stress by 39% and 64% Sardar *et al.,* (2022), respectively, compared with those without Se treatment, thereby reducing Fig.(30).

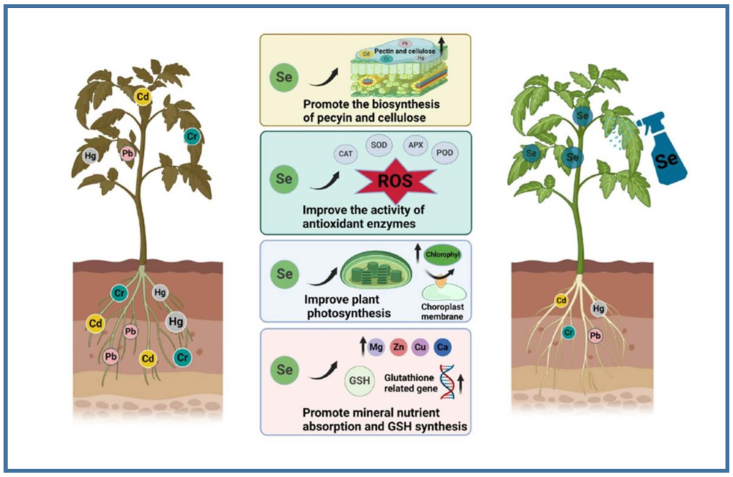


Fig. 30: Illustrates the mechanism of Selenium to alleviate heavy metal stress in plants.

The mitigating effect of selenium on heavy metal stress in plants can be attributed to multiple mechanisms. First, selenium facilitates the production of substances, such as cellulose and pectin, in the cell wall, thereby reducing the absorption of heavy metals. Second, Selenium enhances the antioxidant capacity of plants, thereby mitigating oxidative damage. Additionally, Selenium promotes photosynthesis by supporting chlorophyll synthesis and protecting the structure of chloroplast membranes. Finally, Selenium increases the content of glutathione and essential mineral nutrients in plants, further alleviating heavy metal stress Fig. (31). Cadmium, a common soil pollutant, has been found to accumulate in soil over time, causing detrimental effects on plant growth and development. Studies have shown that the ionization and coordination of Cd can interfere with crucial biochemical reactions within plant cells, disrupting processes such as photosynthesis, respiration, nutrient and water absorption, cell division, nitrogen metabolism, and protein expression. This ultimately leads to the disruption of plant metabolic functions (He *et al.,* 2015).

On the other hand, Selenium, a beneficial element for plant growth, has gained significant attention for its role in promoting plant growth through increased accumulation of carbohydrates and plant hormones, as well as its ability to protect plants against biotic and abiotic stresses (Zhao *et al.,* 2019). One notable benefit of Selenium is its ability to mitigate Cd stress in plants. This is achieved by regulating the uptake, translocation, and sequestration of Cd. Furthermore, Se forms complexes with Cd, reducing the absorption of heavy metals by plants (Shanker *et al.,*1996). Research has also shown that Se can enhance plant tolerance to Cd stress by modulating gene expression. In a study conducted on rice (O. sativa) suspension cells exposed to Cd and treated with different concentrations of Se, the expression levels of certain genes (such as OsLCT1, OsNramp5, OsNramp1, OsIRT1, and OsIRT2) were lower in Se-treated rice cells than in untreated cells. Additionally, the uptake of Cd decreased (Cui *et al.,* 2018).

Patterns of Se mitigating heavy metal stress in plants. The left part shows Selenium treatment and the right is non-seleniferous treatment in plants under heavy metal stress. Selenium enhances osmotic protection. It can enhance the proline and soluble sugar contents and help maintain the stability of the plasma membrane in plants under heavy metal stress (Sardar *et al.,* 2022). Proline enhances membrane stability and reduces the degradation of proteins and carbohydrates (Zhang *et al.,* 2016). Soluble sugars are important osmotic protectants for plants (Afzal *et al.,* 2021). Application of low concentrations of SeNPs (126.6 μmol L^{-1}) effectively enhances the proline content and total soluble sugar content of C. sativum under Cd stress by 39% and 64% Sardar *et al.,* (2022), respectively, compared with those without Se treatment, thereby reducing the metal toxicity of Cd. Further studies have demonstrated that Se enhances the Cadmium retention capacity of cell walls. This effectively reduces the Cadmium content within plant cells, subsequently diminishing the absorption and accumulation of Cadmium by plants (Zhao *et al.,* 2019). The cell wall serves as the first barrier against Cadmium ingress into plants. It is composed of three layers: the intercellular layer, primary wall, and secondary wall. The middle lamella primarily consists of pectin, while the primary wall mainly consists of cellulose, hemicellulose, and pectin. The secondary wall is primarily composed of cellulose and lignin (Bailey, 1938). These components contain functional groups, such as hydroxyl, carboxyl, thiol, and other negatively charged groups that are capable of attracting and binding Cadmium ions to form stable compounds (Parrotta *et al.,* 2015). This facilitates the deposition of Cadmium ions within the cell wall.

Research has indicated that more than 80% of Cadmium in maize (Zea mays) and rice (O. sativa) is adsorbed onto the cell wall (Yu *et al.,* (2021). Research has demonstrated that the application of Se leads to an increase in the biosynthesis of various components, such as pectin, cellulose, hemicellulose, and lignin, in root cell walls. This enhancement facilitates greater sequestration of Cadmium within the cell wall and subsequently alleviates Cadmium -induced stress. Moreover, Se treatment increased the content of pectin and activated pectin methyl esterase in rapeseed (B. napus) plants under Cadmium stress Wang *et al.,* (2023). This increase in pectin content promoted the binding of carboxyl groups to Cadmium, resulting in a reduction in the proportion of soluble Cadmium within the plant cells Yang *et al.,* (2022). Furthermore, Selenium supplementation led to an increase in the pectin and hemicellulose contents in rapeseed (B. napus) plants under Cadmium stress, resulting in a significant reduction in the proportion of soluble Cadmium within the cells (Zhao *et al.,* 2019). These findings were further confirmed in a study on winter wheat (T. durum), highlighting the beneficial role of Se in both plant growth and the reduction in Cadmium uptake (Di *et al.,* 2023). Hence, it can be concluded that Se plays a crucial role in enhancing the tolerance of plants to Cadmium stress.

Sun *et al.* (2016) demonstrated that Se application could reduce Cd-induced phytotoxic effects on cucumber plants by regulating stress response-related proteins and pathways, such as glycolysis pathway and nitrate assimilation pathway, which may increase Cd tolerance. Selenium reduces the uptake and translocation of heavy metals in plants. Selenium promotes the formation of Fe plaques around the roots of plants under Hg stress Fu *et al.,* (2018), thus hindering heavy metals from entering the roots and accumulating in plants. Zhou and Li found that Selenium increases the adsorption of Hg^{2+} by Fe plaques in rice and causes an average of 1.42-fold increase in Selenium -treated plants compared with non-seleniferous plants (Zhou *et al.,* 2020). Moreover, Selenium interacts with heavy metals. Thus, Selenium application leads to the formation of inert HgSe or/and HgSe-containing proteinaceous complexes in the rhizosphere (Tran *et al.,* 2021). For instance, Selenium forms insoluble HgSe precipitates with Hg in the roots, thus reducing the mobility and availability of Hg Fu *et al.,* (2018) Fig. (31).

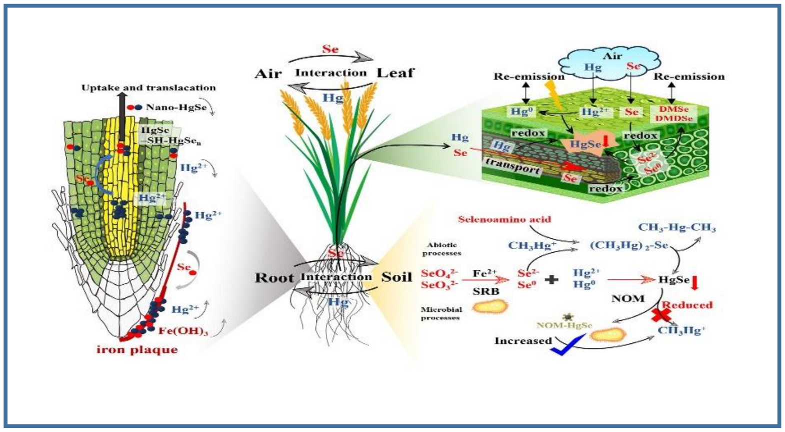


Fig. 31: Illustrates selenium reduces the levels of methylmercury (MeHg), a carcinogen in rice. After Wang *et al.,* (2016).

Selenium reduces the levels of methylmercury (MeHg), a carcinogen in rice. The reduction in soil MeHg concentrations could be mainly attributed to the formation of Hg-Se complexes and thus reduction of microbial MeHg production (Wang *et al.,* 2016). Selenium can inhibit the translocation of heavy metals. The addition of selenite can significantly decrease the Cadmium concentrations in xylem sap, suggesting that Selenium can reduce Cadmium levels in the rice shoots by inhibiting Cadmium translocation from the roots to the shoots. This phenomenon could be ascribed to the increasing formation of Cadmium -thiol complexes in the roots and the reduction of Cd transport to the shoots Zhao *et al.,* (2013). Selenium can inhibit the translocation of heavy metals Zhao *et al.,* (2013) because Selenium promotes the formation of heavy metal-thiol complexes, thereby reducing heavy metals in the xylem sap and the transfer of heavy metals from the roots to the shoots (Wan *et al.,* 2019) . The common thiol compounds in plants include GSH, metallothionein, and phytochelatin (PCs) Yadav (2010), Dalcorso *et al.,* (2008), such complexes formed by PCs and heavy metals and transferred into the vacuoles.

4.9. Regulation of plant hormones

Recently, interest in controlling plant hormones with phyto-synthesized NPs to improve plants' capacity to withstand drought stress has been increasing. Researchers have determined the critical functions of various plant hormones in the responses of plants to stress, including abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA). Wang *et al.* (2020) stated that Jasmonic acid (JA) is an endogenous growth-regulating substance, initially identified as a stress-related hormone in higher plants. Similarly, the exogenous application of JA also has a regulatory effect on plants Fig. (32). Abiotic stress often causes large-scale plant damage. In this review, we focus on the JA signaling pathways in response to abiotic stresses, including cold, drought, salinity, heavy metals, and light. On the other hand, JA does not play an independent regulatory role, but works in a complex signal network with other phytohormone signaling pathways. In this review, we will discuss transcription factors and genes involved in the regulation of the JA signaling pathway in response to abiotic stress. In this process, the JAZ-MYC module plays a central role in the JA signaling pathway through integration of regulatory transcription factors and related genes. Simultaneously, JA has synergistic and antagonistic effects with abscisic acid (ABA), ethylene (ET), salicylic acid (SA), and other plant hormones in the process of resisting environmental stress.

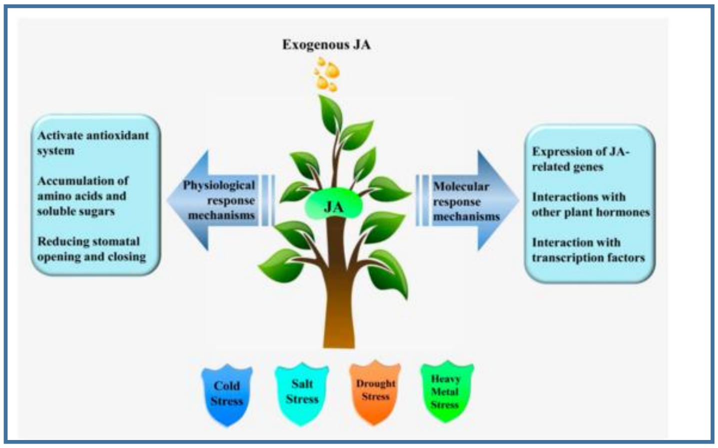


Fig. 32: The role of jasmonic acid (JA) in plant response to abiotic stress. After Wang *et al.,* (2020)

The amounts of these hormones can be influenced by phyto-synthesized NPs when plants are stressed by drought, potentially causing the plants to respond (Ayyaz *et al.,* 2022; Sutulien *et al.,* 2023; Castroverde and Dina, 2021). Due to their numerous applications in industries, including agriculture and environmental cleanup, phyto-synthesized NPs have emerged as a promising study field, which also plays a significant role in plant hormonal regulations (Ku *et al.,* 2018; Zhang *et al.,* 2022; Li *et al.,* 2021). Recently, interest has increased in employing phyto-synthesized NPs to regulate plant hormones and improve plants' resistance to drought stress.

Tripathi *et al.* (2022) reported that in the era of climate change, plants are facing various and unprecedented environmental stresses. Both biotic and abiotic stress factors are very important constraints that adversely affect the plants' developmental and metabolic processes. In order to cope with the environmental challenges, plants have evolved a variety of defense mechanisms at various levels by modifying their morphological, physiological, anatomical, biochemical features up to molecular level. Currently, nanotechnology is a blooming innovative area in the field of plant science with new ideas for understanding the appropriate mechanism of plants survival under stress. Nanoparticles are regarded as regulatory molecules for plants that can modulate a wide range of physiological and biochemical processes along with activation of the anti-oxidative defense system, hormonal regulation, and stress-related gene expression.

The plant growth hormones also act as stress regulatory molecules and known to involve in various signaling cascades under the exposure of nanoparticles. Under the stress, over production of reactive oxygen species (ROS) are measured which can be regulate with the help of nanoparticles. Recently, few studies reported that nanoparticles could ameliorate the stress consequences with the regulation of phytohormones signaling. However, the appropriate mechanism of crosstalk between nanoparticles and phytohormones biosynthesis is still at infancy stage. Thus, it is required to understand the nanoparticles-related regulation of phytohormones synthesis and their signaling under stress conditions for the advancement and sustainability of plant production. In this review, we are elucidating the crosstalk of nanoparticles and phytohormones along with their potential regulatory role under plant stress conditions (33), (34).

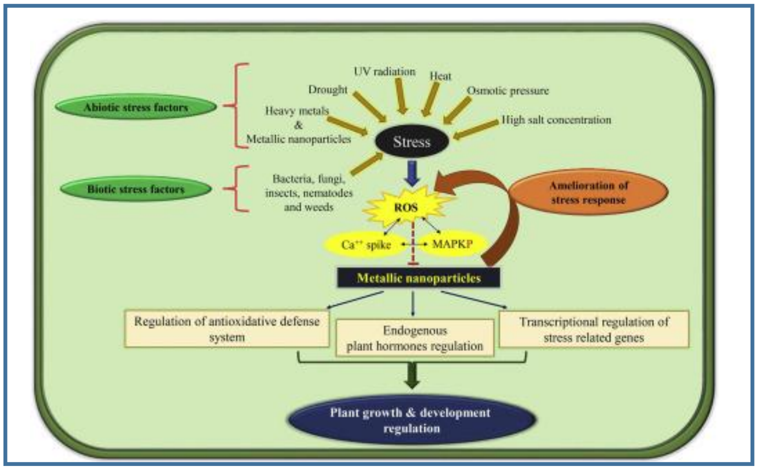


Fig. 33: Illustrates the systematic representation of nanoparticles related general regulatory mechanism for amelioration of different stress responses in plants. After Tripathi *et al.,* (2022).

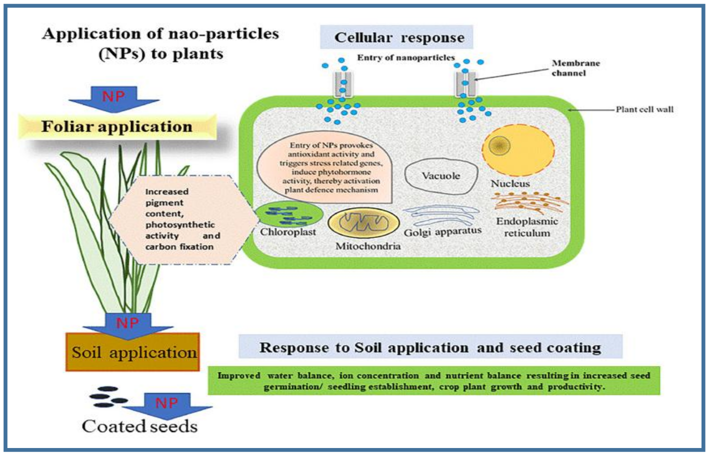


Fig. 34: Delivery of NPs to plants either by soil application, seed coating, or foliar spray to protect plants against abiotic stresses (a) NPs can be either applied through foliar spray or application in the soil or as seed coating (b) mode of up-take (c) translocation of NPs in plants. Adapted from Manzoor *et al.,* (2022).

Tripathi *et al.* (2022) reported nanoparticles regulated phytohormones biosynthesis and signaling in plants, including auxin, gibberellins, cytokinin, abscisic acid (ABA), ethylene, brassinosteroids, salicylic acid (SA), and jasmonic acid (JA). Among these hormones, auxin, gibberellin, and cytokinin are known to play major roles in plant developmental responses; while ABA, SA, JA and ethylene are involved in modulation of plant defense responses against biotic and abiotic constrains (Khan *et al.,* 2020; Sytar *et al.,* 2019). Nanoparticles can primarily regulate the protective responses (as plant growth regulators signaling) of plants via synergistic and antagonistic actions, are referred to as signaling cross talk. These molecules or different ones that may follow the above generic pathway initiate a subsequent round of signaling.

In the last decades, some of the studies have been conducted on how stress signals are perceived by plants and the plant growth regulators are affected. In the plants, nanoparticles may control phytohormones responses at various points, such as by regulating the biosynthesis of a given phytohormone, by modifying the available pool of phytohormone and by regulating signaling process (Rasool, 2022; Verma *et al.,* 2016). Although, nanoparticles mediated responses are depending upon various factors likely on type of nanoparticles, plant species, and exposure conditions etc. (Yue *et al.,* 2017). Studies carried out so far have provided evidence about the underlying interactions between nanoparticles and plant growth hormones (Vankova *et al.,* 2017; Xie *et al.,* 2020). However, studies about molecular mechanism related to nanoparticles and phytohormones crosstalk is still required.

Rajaee Behbahani *et al.* (2020) investigated stimulated root development and embryo-like structures formations during the callogenesis / organogenesis of Momordica charantia, treated with nano-selenium via nanoparticles mediated changes in phytohormones with NO/H_2S signaling. They have suggested that the inhibition of xylem tissue differentiation, stem bending, inhibition of primary root development, and appearance of adventitious roots indicated hormonal changes, (especially ethylene and auxin) under nano-Se exposure and recommended to investigate nanoparticles mediated phytohormonal changes up to molecular level, in near future. The present section deals with the regulation of phytohormones with nanoparticle exposure.

Fahima *et al.* (2023) reported that abiotic stress globally has imposed the sternest environmental issues that enforce a significant impact on agricultural food production. Particularly, salinity, drought, heavy metal, and extreme high and low temperature are the principal components of abiotic stresses. The majority of the agricultural land is altered by the stresses and impacted by the reduction of production. An environmental stress response is internally governed by intricate biochemical and molecular signal transduction events that act in an orchestrated manner for determining the tolerance or sensitivity of the plants. With exposure to abiotic stress, plants respond by reprogramming the interconnected defense networks and metabolic pathways. The variety of agrarian, physiological practices and genetic engineering methods are adapted for promoting plant stress adaptability. With the advent of nanotechnology, its application in agriculture has emerged as a valuable tool to reach the goal of sustainable food production worldwide. Nanoparticles possess unique physicochemical properties that allow them to interact with biological systems in a specific manner in terms of size, large surface area, surface charge, etc. In this regard, numerous studies have been carried out to study the efficacious role of nanoparticles in strengthening plant stress resilience. In this review, we will discuss the molecular mechanisms governing the nanoparticle mediated stress response to increase the potentiality of cultivated plants.

These nanoparticles are made from plant extracts, which serve as sustainable and eco-friendly reducing and stabilizing agents, providing a more environmentally friendly option to conventional chemical processes (Devi *et al.,* 2023; Santhosh *et al.,* 2022). The passage also emphasizes the crucial functions of abscisic acid (ABA), salicylic acid (SA), and jasmonic acid (JA) as essential participants in how plants react to stress. These phyto-synthesized NPs can remarkably regulate the levels of these hormones in response to drought stress, which may lead to the onset of adaptive responses in plants. Abscisic acid (ABA) has a significant and multifaceted function in how plants respond to stress, particularly in drought-like conditions. Controlling stomata closure, which aids plants in water conservation by lowering transpiration, is one of its primary roles (Waadt *et al.,* 2022; Ulhassan *et al.,* 2022; Sutulien *et al.,* 2023; Li *et al.,* 2021 Fig. (35).

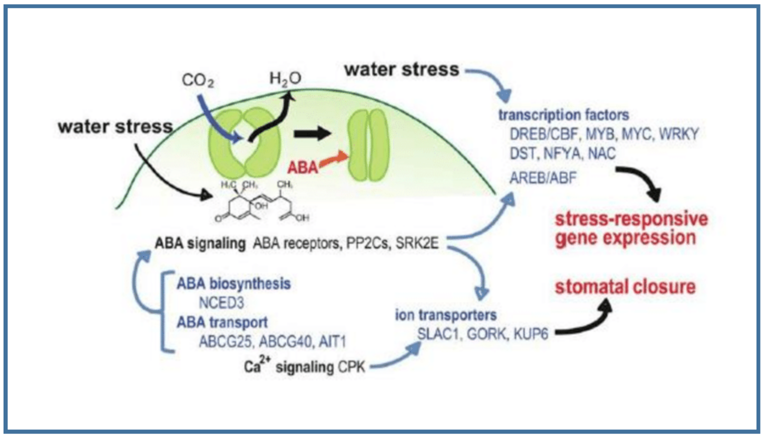


Fig. 35: Illustrates the closure of stomata by the effect of abscisic acid (ABA) in the plant exposed to the stress. After Hüseyin and Hüdaverdi (2018).

Hüseyin and Hüdaverdi (2018) stated that during drought, photosynthesis decreases due mainly to two reasons; stomatal limitations that occur due to stomatal closure upon moderate water deficit conditions and other limitations that generally occurs upon longer and more severe water stresses Fig. (35). One of the earliest responses against drought is stomatal closure that limits CO_2 diffusion towards chloroplasts Lima, (2002). During drought two main reasons to cause plants to close, their stomata are hydrolic signals (leaf water potential, cell turgor) and chemical signals (Abscisic acid; ABA). Abscisic acid (ABA), synthesized in the roots can also be transport via transpiration stream, induces stomatal closure under drought stress conditions (Teiz, (1998). It has been found that photosynthetic electron transport and photophosphorylation capacities decrease in chloroplasts of plants that are exposed to severe water deficit reduce (Smirnoff, 1993). Photosystems in chloroplasts, particularly PSII, are affected by drought stress (He, 1995). Other limitation of photosynthesis may be related to the oxidative damage to chloroplast lipids, pigments or proteins (Tambussi, 2000). Photosynthetic capacity in plants varies depending on the content of water within the cell.

When plants are under drought stress, phyto-synthesized NPs can help them conserve water by boosting the levels of ABA. As a signaling molecule, ABA also affects the expression of several genes involved in the stress response. This complex gene regulation system improves the plant's capacity to withstand and respond to adverse environmental conditions, ultimately fostering drought resistance (Zhao *et al.,* 2022). Although salicylic acid (SA) is widely established to protect plants from biotic stresses, it has recently attracted interest for its ability to help plants in abiotic and drought stresses, (Castroverde and Dina, 2021). Previous research shows that salicylic acid (SA) protects plants against drought-related damage. It can be affected by phyto-synthesized NPs. For plants to appropriately respond to water constraints, a sophisticated signaling network formed by SA and other stress-related hormones is necessary (Mozafari *et al.,* 2018; Pandey *et al.,* 2023). Jasmonic acid (JA), particularly in drought adaptation, is a crucial aspect of the plant's toolset for managing stress. A series of reactions brought on by regulating JA levels by phyto-synthesized NPs activate genes and signaling pathways linked to drought responses.

As a result, the plant can better manage water scarcity and endure adverse environmental circumstances. A fascinating area of study is the relationship between phyto-synthesized NPs and JA signaling, which has the potential to lead to the development of brand-new, groundbreaking techniques for improving drought tolerance in plants and advancing environmentally friendly farming methods, as shown in (Zohra *et al.,* 2022; Ikram *et al.,* 2021). Chandrashekar *et al.* (2023) stated that drought stress remains one of the most detrimental environmental constraints that hampers plant growth and development resulting in reduced yield and leading to economic losses. Studies have highlighted the beneficial role of carbon-based nanomaterials (NMs) such as multiwalled carbon nanotubes (MWNTs), single-walled carbon nanotubes (SWNTs), graphene, fullerene, and metal-based nanoparticles (NPs) (Ag, Au, Cu, Fe2O3, TiO2, and ZnO) in plants under unfavorable conditions such as drought. NPs help plants cope with drought by improving plant growth indices and enhancing biomass. It improves water and nutrient uptake and utilization. It helps retain water by altering the cell walls and regulating stomatal closure.

The photosynthetic parameters in NP-treated plants reportedly improved with the increase in pigment content and rate of photosynthesis Fig. (36). Due to NP exposure, the activation of enzymatic and nonenzymatic antioxidants has reportedly improved. These antioxidants play a signifcantly role in the defense system against stress. Studies have reported the accumulation of osmolytes and secondary metabolites. Osmolytes scavenge reactive oxygen species, which can cause oxidative stress in plants. Secondary metabolites are involved in the water retention process, thus improving plant coping strategies with stress. The deleterious effects of drought stress are alleviated by reducing malondialdehyde resulting from lipid peroxidation. Reactive oxygen species accumulation is also controlled with NP treatment. Furthermore, NPs have been reported to regulate the expression of drought-responsive genes and the biosynthesis of phytohormones such as abscisic acid, auxin, gibberellin, and cytokinin, which help plants defend against drought stress

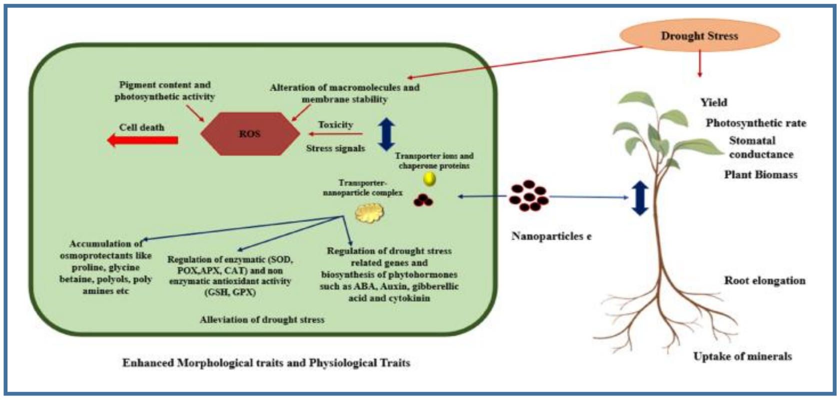


Fig. 36: Impact of nanoparticles on plant and cells under drought stress including signalling pathways such as regulation of defense mechanism, antioxidant activity and drought responsive genes and biosynthesis of phytohormones. Drought exposure triggers the accumulation of Reactive Oxygen Species (ROS) that causes oxidative stress. ROS alters the macromolecules in the cytoplasm and degrades the cell membrane. In addition, it decreases the pigment content thus reducing the photosynthetic activity. Prolonged oxidative stress ultimately leads to cell death. Overall effects of drought can be seen on the plant including reduced yield, wilting, stunted growth and plant death. The nanoparticles upon treatment enter the cell and form a complex with transporter ions and regulate the accumulation of osmoprotectants, increase the activity of antioxidants, biosynthesis of hormones and regulation of drought responsive genes. Adopted and Modified from Jalil and Ansari (2019).

1- Effect of Selenium on plant growth

Selenium has been found to have a growth-promoting role, which is the result of improved physiological characteristics. Its treatment can stimulate a number of plant growth cascades, such as germination, yield, and nutritional quality at lower concentrations, but at higher doses, it can be harmful. Selenium regulates plant senescence, fruit ripening, fruit quality, and flavor by regulating the biosynthesis of ethylene (Ryant *et al.,* 2020) Fig. (37).

Khan *et al.* (2023) stated that Selenium, being an essential micronutrient, enhances plant growth and development in trace amounts. It also protects plants against different abiotic stresses by acting as an antioxidant or stimulator in a dose-dependent manner. Knowledge of Selenium uptake, translocation, and accumulation is crucial to achieving the inclusive benefits of Selenium in plants. Therefore, this review discusses the absorption, translocation, and signaling of Selenium in plants as well as proteomic and genomic investigations of Selenium shortage and toxicity.

Furthermore, the physiological responses to Selenium in plants and its ability to mitigate abiotic stress have been included. In this golden age of nanotechnology, scientists are interested in nanostructured materials due to their advantages over bulk ones. Thus, the synthesis of nano-Se or Se nanoparticles (SeNP) and its impact on plants have been studied, highlighting the essential functions of Se NP in plant physiology. In this review, we survey the research literature from the perspective of the role of Selenium in plant metabolism.

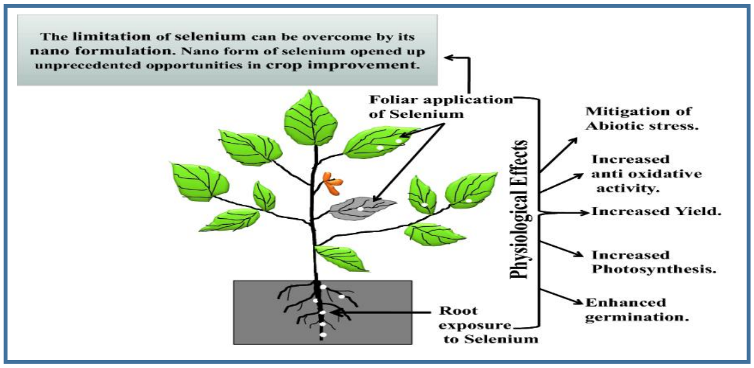


Fig. 37: Illustrates the role of selenium in plant physiology. After Khan *et al.,* (2023)

Furthermore, Se maintains the structure, function, and contents of cells and acts as an anti-senescent agent (Kaur *et al.,* 2014). The application of 0.5 mg/kg Se-engineered nanomaterial (ENM) enhanced Se content and yield by 338.0 and 19.8%, respectively in *Brassica chinensis*. The supplementation of Se ENM increased Selenium content in *Brassica chinensis* up to 32.8 µg/100 g, which could provide the daily recommended Se intake for humans (Wang *et al.,* 2022a,b). The application of Se increased antioxidative activity, glutathione and protein levels. In addition to this, it enhanced rice yield (7.58%) and downregulated MDA, and proline contents. It also improved thiol and rutin metabolism-related enzymes, enhanced the uptake of Fe, Mn, Co, Cu, Zn, and Mo, and thus improved plant growth. Selenium can replace S in the sulfhydryl (-SH) group on cysteine to form selenocysteine (SeCys) (Roman, 2016). It also protects plants against pathogens as mentioned by Quinn *et al.* (2010).

When exogenous Selenium concentration was controlled at 30 and 50 mg/kg, foliar application of Se could effectively increase the 100-bud weight (weight of one hundred growing buds) of tea trees. The 100-bud weight gradually increased with the spraying dosage and gradually decreased with the spraying dosage at 100 mg/kg. This finding suggests that, with a proper concentration of Selenium treatment, tea yield might be greatly enhanced (Huang *et al.,* 2020).

Cheng *et al.* (2024) reported that Lettuce (*Lactuca sativa*) is rich in vitamins, minerals, and bioactive components, serving as an important source of selenium intake for humans. Studies investigated that the effects of Selenium treatment on lettuce using different concentrations of sodium selenite (Na_2SeO_3), on biomass, physiological indicators, nutritional composition, and physiological changes.

Application of Na_2SeO_3 on hydroponics experiment showed that plant biomass of lettuce with low concentrations of Na_2SeO_3 has a stimulatory effect on the growth of lettuce. When 0.5–1.5 mg/L of Na_2SeO_3 was added to the culture solution, both the shoot and root lengths of the plants increased compared to the control group (Fig. 38a). Compared to the control, treatment with 0.5, 1, and 1.5 mg/L of Na_2SeO_3 significantly increased root lengths by 14.3%, 21.2%, and 52.5%, respectively, while shoot lengths were significantly increased by 43.4%, 53.3%, and 91.0%, respectively. However, the lengths of both the shoot and root decreased after treatment with a 2 mg/L solution of Na_2SeO_3. As shown in (Fig. 38 b), the biomass of lettuce treated with 0.5–1.5 mg/L of Na_2SeO_3 solutions increased significantly, by 50.5%, 70.6%, and 158%, respectively. However, the biomass of lettuce treated with a 2 mg/L solution of Na_2SeO_3 decreased.

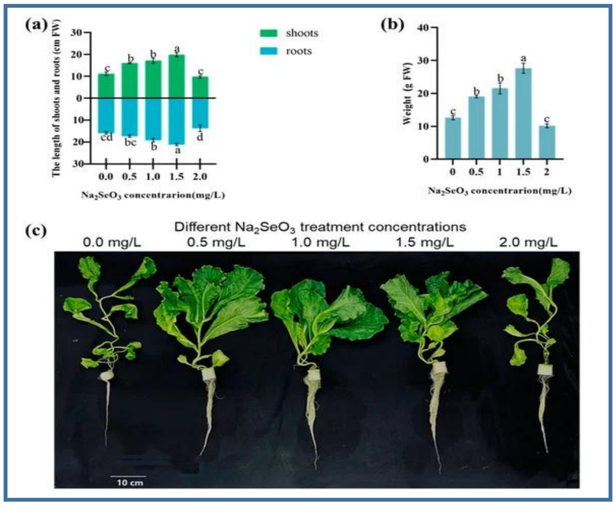


Fig. 38: The effects different concentrations of Na_2SeO_3 on the length and biomass of lettuce above and below ground. (**a**) Length of shoot and root portions of lettuce. (**b**) Biomass of lettuce. (**c**) Growth status of lettuce, with white scale bars representing 10 cm length. The bar charts are adorned with error bars representing the standard error of the mean, calculated from a sample size of three ($n = 3$). Additionally, various letters are employed to designate statistically significant disparities in the mean values, as determined by Duncan's multiple range test, with a significance of $p < 0.05$. After Cheng *et al.,* (2024)

On the other hand, the contents of chlorophyll and carotenoids in lettuce treated with different concentrations of selenite were higher than those in the control treatments Fig. (39), with significant increases only observed in the 0.5 mg/L treatment as compared to the control one. Specifically, chlorophyll (A) increased by 1.14-fold (Fig. 39a), chlorophyll (B) increased by 54.0% (Fig. 39b), carotenoids increased by 1.65-fold (Fig. 39c), and total chlorophyll increased by 91.5% (Fig. 39d). While the contents in the other treatment groups were also higher than the control, these increases were not statistically significant.

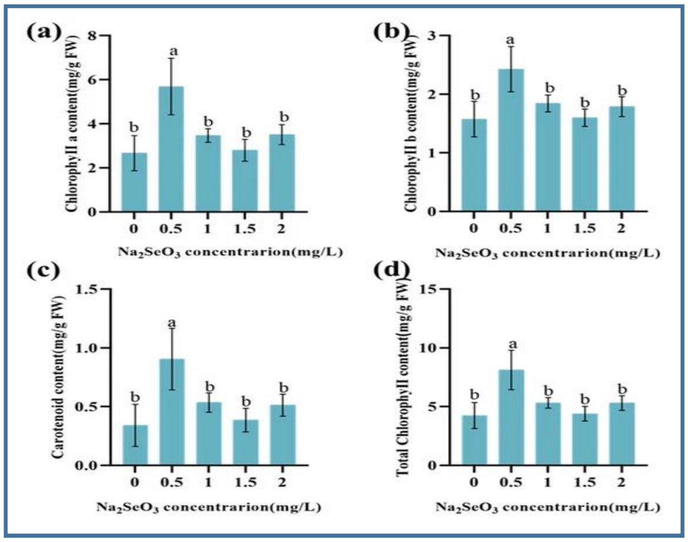


Fig. 39: Impact of varying concentrations of Na_2SeO_3 treatment on photosynthetic pigments and Carotenoid content in lettuce. (**a**) Chlorophyll a content. (**b**) Chlorophyll b content. (**c**) Carotenoid Content. (**d**) Total chlorophyll content. Error bars in each subfigure represent the standard error of the mean (n = 3), indicating the reliability and precision of the measurements. Different letters above the bars indicate significant differences in the mean values based on Duncan's multiple range test ($p < 0.05$), allowing for a statistical comparison across the treatment groups. After Cheng *et al.,* (2024)

Comparing to the control treatments, the vitamin- C content in lettuce treated with Na_2SeO_3 slightly decreased, but the difference was not statistically significant (Fig. 40a). Treatment with 0.5, 1, and 1.5 mg/L of Na_2SeO_3 increased the soluble sugar content in lettuce leaves, with the 0.5 mg/L treatment resulting in a significant elevation of 37.8%. However, when treated with 2 mg/L of Na_2SeO_3, the soluble sugar content in lettuce decreased significantly by 19.8% (Fig. 40b). After treatment with 0.5 mg/L of Na_2SeO_3, the soluble protein content in lettuce increased significantly (by 63.1%) compared to the control group, while the other concentrations showed slightly higher levels but without significant differences (Fig. 40c). Compared to the control, the flavonoid content in the 0.5 mg/L and 1.5 mg/L Na_2SeO_3 significantly increased, by 14.6% and 34.8%, respectively. At a concentration of 1.0 mg/L, the flavonoid content decreased slightly but not significantly (Fig. 40d).

Compared to the control group, the total phenolic content in the 0.5 and 1.0 mg/L Na_2SeO_3 treatment groups increased significantly, by 21.6% and 20.4%, respectively. However, at a concentration of 2 mg/L, the total phenolic content decreased significantly, by 29.6% (Fig. 40e). Treatment with 0.5 mg/L of Na_2SeO_3 significantly enhanced the anthocyanin content in lettuce, increasing it by 70.3% as compared to the control. However, treatments with 1.0 mg/L, 1.5 mg/L, and 2 mg/L of Na_2SeO_3 reduced the anthocyanin content in lettuce, but the differences were not statistically significant (Fig. 40f).

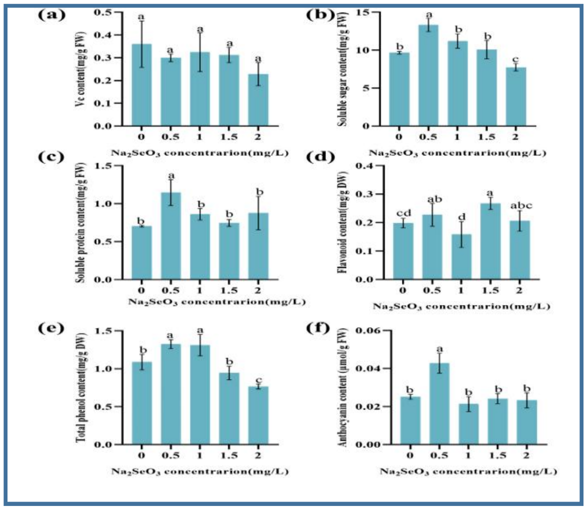


Fig. 40: Impact of Na_2SeO_3 treatment on the nutritional composition of lettuce. (**a**) Vc content. (**b**) Soluble sugar content. (**c**) Soluble protein content. (**d**) Flavonoid content. (**e**) Total phenolic Content. (**f**) Anthocyanin content. Error bars in each subfigure represent the standard error of the mean (n = 3), providing a measure of the reliability and precision of the measurements. Different letters above the bars indicate significant differences in the mean values based on Duncan's multiple range test ($p < 0.05$). After Cheng *et al.,* (2024)

Results noticed the application of lettuce with 1.0 mg/L of Na_2SeO_3, significantly decreased its MDA content (by 35.1%) as compared to the control one. However, upon treatment with 1.5 mg/L and 2 mg/L of Na_2SeO_3, the MDA content in lettuce leaves rose significantly, increasing by 99.8% and 21.8%, respectively (Fig. 41). The application of Na_2SeO_3 significantly influenced the GSH content and the activity of antioxidant enzymes in lettuce leaves (Fig.41). Treatment with 0.5 mg/L and 1.0 mg/L of Na_2SeO_3 resulted in an increase in GSH content in lettuce leaves, with the 1 mg/L concentration exhibiting a significant increase of 19.0%. Conversely, higher concentrations of Na_2SeO_3 caused damage to the lettuce leaves, as GSH content decreased in the 1.5 mg/L and 2.0 mg/L treatment groups, with the 2.0 mg/L treatment group experiencing a significant decrease of 19.8% (Fig. 41a).

Compared to the control group, the SOD activity in lettuce leaves treated with 0.5 mg/L, 1.0 mg/L, and 1.5 mg/L of Na_2SeO_3 was significantly higher, increasing by 14.9%, 22.4%, and 19.3%, respectively. However, at a concentration of 2.0 mg/L, the SOD activity in the treated lettuce leaves decreased to the level of the control group (Fig. 41b). Furthermore, treatment with 1.0 mg/L and 1.5 mg/L of Na_2SeO_3 significantly elevated the POD activity in lettuce, increasing by 13.26-fold and 2.76-fold, respectively (Fig. 41c). Notably, following Na_2SeO_3 treatment, all treatment groups exhibited significantly higher CAT activity compared to the control group, with increases of 1.20-fold, 1.25-fold, 1.07-fold, and 91.3%, respectively (Fig. 41d).

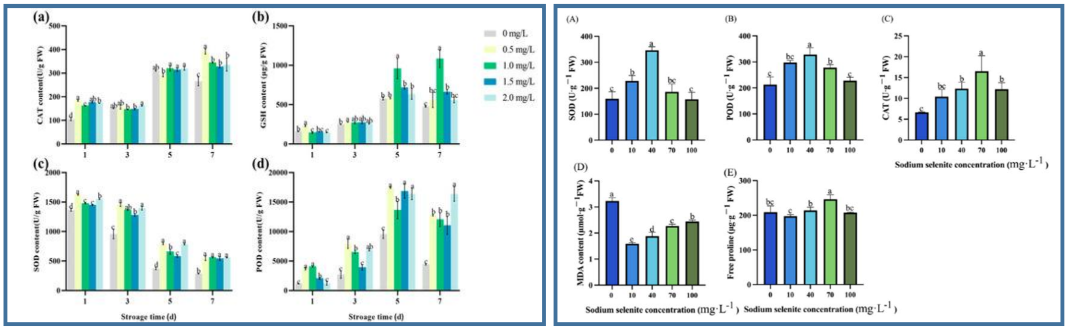


Fig. 41: The effects of Na_2SeO_3 treatment at varying concentrations on the activities of antioxidant Enzyme in lettuce. (a) GSH content in various treatment groups. (b) SOD activity. (c) POD activity. (d) CAT activity. The error bars depict the standard error of the mean (n = 3), whereas distinct letters Denote significant disparities in the mean values, determined through Duncan's multiple range test ($P < 0.05$). After Cheng *et al.,* (2024)

Safflower genotypes with Selenium treatments had significant improvements in plant height, number of heads per plant, grain yield, and biological yield (total biomass). It also enhanced oil quality. The highest values were obtained at 200 mg. L^{-1} foliar applied Selenium, which was statistically comparable to 150 mg.L^{-1} .Selenium application for grain yield and oil quality Sher *et al.,* (2022) Figs. (42, 43).

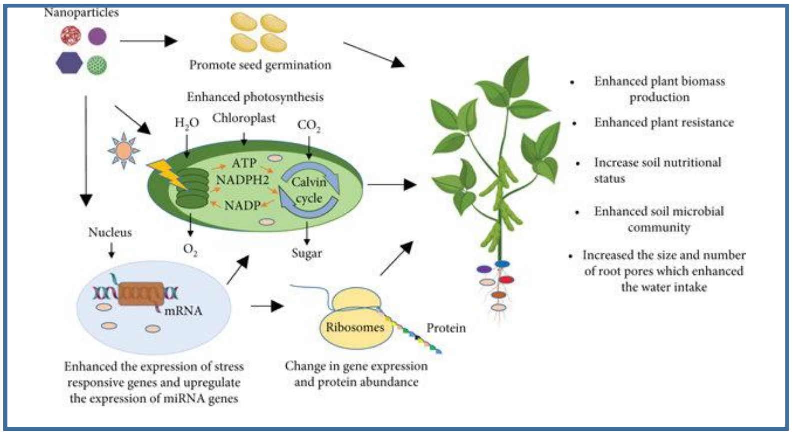


Fig. 42: Illustrates the positive effects of nanoparticles on plant growth and development. The optimum concentration of nanoparticles causes an alteration in different physiological processes to increase seed germination and photosynthesis of the plants. Further, the nanoparticles alter the gene expression of different genes and miRNAs that have a positive impact on stress tolerance and plant biomass. After Shahid Ali *et al.,* (2021)

Shahid Ali *et al.* (2021) stated that nanotechnology has shown promising potential tools and strategies at the nanometer scale to improve food production and meet the future demands of agricultural and food security. However, considering nanotechnology's potential benefits to date, their applicability has not yet reached up to field conditions. Increasing concerns regarding absorption, translocation, bioavailability, toxicity of nanoparticles, and impropriety of the regulatory framework restrict the complete acceptance and inclination of the agricultural sector to implement nanotechnologies. The biological function of nanoparticles depends on their physicochemical properties, the method of application, and concentration. The effects of the various types of nanoparticles (NPs) on plants were determined to increase seed germination and biomass or grain yield. The NPs also increased the plant's resistance to various biotic and abiotic stresses.

The plant's biological functions depend on the events that occur at the molecular level. However, little progress has been made at the molecular level influenced by nanoparticles, which is an important step in evaluating potential mechanisms and plants' effects. Therefore, it is important to understand plants' underlying mechanism and response towards nanoparticles, and the gene expression changes through molecular approaches. The associations of nanomaterials with plant cells, the process of internalization, and the distribution of biomolecules using nanoparticles as a carrier are studied but not well understood. The transmission of biomolecules, such as nucleic acids, is a major obstacle due to cell walls, limiting the application of nanomaterials in crop enhancement mediated by genetic engineering. Recently, the use of different nanomaterials for nucleic acid delivery in plant cells has been published. Here, we aim to update researchers on the absorption and translocation of nanoparticles and elaborate on the importance of nanoparticles in agriculture and crop stress tolerance.

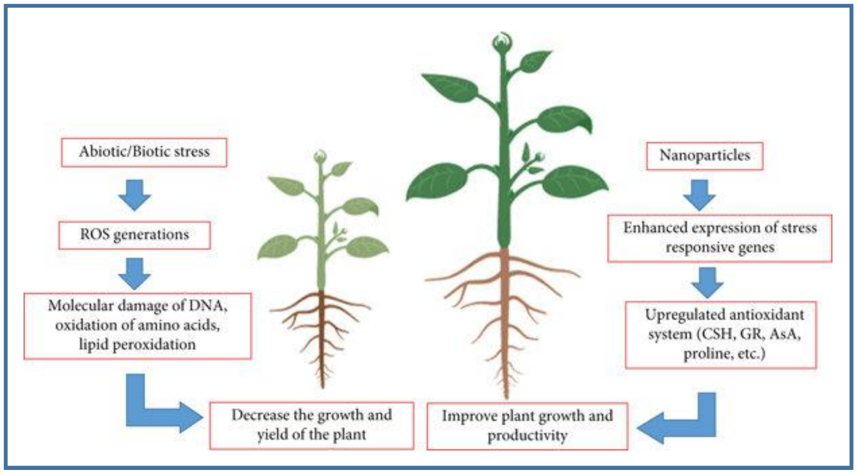


Fig. 43: Illustrates general mechanisms of nanoparticles increase the mitigating ability of plants under different stress environments. After Shahid Ali *et al.,* (2021)

Shekari *et al.* (2019) evaluated the effects of Selenium supplementation on cucumbers cultivated under Cd and Pb stress at various growth stages. The authors found that applications of 4 and 6 mg.L^{-1} of Selenium increased flowering, and improved the ratio of female to male flowers. It also decreased flowering time, and significantly increased fruit yield and production time under stress conditions (60 mM Pb and 100 mM Cd) compared to stressed plants. According to a study by Yin *et al.* (2019), Selenium application to rice roots significantly boosts Se accumulation, photosynthetic rate, biomass accumulation, and tolerance to Cd stress.

Nevertheless, depending on the Se species used for the treatment, the stimulatory effects of Selenium vary. Se-(Methyl) selenocysteine application at the root induced the maximum water extractable Selenium content in leaves during the vegetative stage, with large contributions from organic Selenium species such as Selenium -amino acid and non-amino acid organic Selenium. Further research during the reproductive stage showed that the highest total Se content in rice seeds, which was primarily attributable to inorganic Selenium, was produced by foliar application of sodium selenite (Na2SeO3). On the other hand, Na2SeO3 treatment at the root caused the greatest concentration of healthy organic Selenium molecules. The application of Selenium to rice roots also improved the concentration of critical elements and amino acids while raising antioxidant capability (Yin *et al.,* 2019). Furthermore, a controlled pot experiment was followed by a field experiment over the course of two years on sandy clay loam soil (Inceptisol) in West Bengal, India (Adhikary *et al.,* 2022). They evaluated the efficacy of sodium selenite (Na-selenite), sodium selenate (Na-selenate), zinc oxide nanoparticles (ZnO-NPs), and their combinations as priming agents for direct seeded rice (DSR). Compared to hydro priming, priming using mixtures of all priming agents has demonstrated advantages. All of the combinations in the field trial outperformed the control in terms of plant chlorophyll, phenol, and protein levels. It also enhanced leaf area index, crop growth rate, nutrient uptake (N, P, K, B, Zn, and Si), and DSR yield (Adhikary *et al.,* 2022).

2- Impacts of selenium for improving ion homeostasis under heavy metal toxicity

Although studies related to ion homeostasis in response to Se application under heavy metal stress are available, but the available ones have shown positive results regarding said trait in plants. In response to heavy metal pollution, plants employ a range of mechanisms to withstand the stress caused by heavy metals. Initially, heavy metal ions bind to particles in the soil and subsequently move toward plant roots via water percolation in the soil. Root cell surfaces possess ion channels and internal transport proteins that selectively absorb or exclude specific heavy metal ions, facilitating their transport to other plant tissues and organs (Oyewo *et al.,* 2020; Mitra *et al.,* 2014). Moreover, heavy metal ions in the soil can bind with gelatinous substances on the surface of plant roots, resulting in deposits that impede or prevent the further movement of heavy metal ions into the plant. This barrier process aids in reducing the uptake of highly concentrated heavy metals from the soil, thereby minimizing their toxic effects on plants (DaCorso *et al.,* 2013).

At the cellular level, heavy metals primarily interact with the cell wall of plant cells through physical adsorption or chemical bonding. Components such as pectin and cellulose in the cell wall possess a high affinity for heavy metal ions, leading to their binding and formation of complexes or precipitates. This immobilizes heavy metal ions on the surface of the cell wall (Figure 1), limiting their entry into the cell and thus mitigating their harmful effects on plant cells (Krzesłowska, 2011). A fraction of the heavy metal ions will permeate the membranes of root hair cells, entering the cytoplasm through Fe carrier proteins, ion channels, and ion pumps (Yang *et al.,* 2022). Subsequently, within the cytoplasm, transport proteins facilitate the further transport of heavy metal ions to different organelles, including chloroplasts, mitochondria, and the endoplasmic reticulum Fig. (44). The accumulation of heavy metal ions in these organelles significantly contributes to their toxicity. For instance, metallothionein in chloroplasts can bind heavy metal ions, forming stable chelates, thereby alleviating the detrimental effects of heavy metal ions on chloroplasts and minimizing their impact on photosynthesis (Zhang *et al.,* 2020). Additionally, intracellular chelators, such as glutathione (GSH), are utilized by plant cells to form complexes with heavy metal ions, reducing their toxicity. This chelation process aids in stabilizing heavy metal ions, which are subsequently transported to the cell wall or roots for excretion through transport proteins (Hossain *et al.,* 2012).

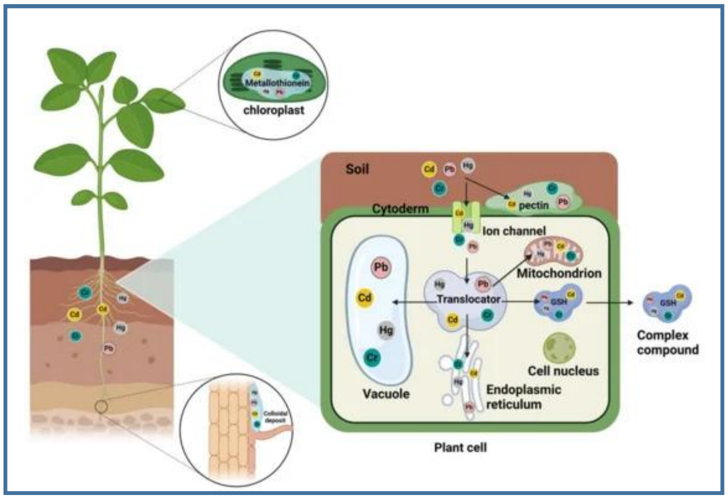


Fig. 44: Illustrates heavy metals entering plant cells and their transport process. After Yuan *et al.,* (2024)

Excessive uptake of heavy metals by plants results in heavy metal accumulation in plant tissues, causing subsequent changes in gene expression. Genes linked to antioxidant defense, ion balance, and detoxification pathways are activated to enhance resistance to heavy metal ions (Syta *et al.,* 2013). Additionally, plants adjust their metabolic pathways to cope with heavy metal ion stress. These enzymes activate antioxidant enzyme systems to reduce oxidative damage, regulate ion channels and pumps to maintain ion balance, and modulate secondary metabolite synthesis to minimize damage caused by heavy metal ions. These response mechanisms enable plants to mitigate the toxic effects of heavy metal ions, enhance tolerance, and maintain cellular environment stability and normal functions (Lynes *et al.,* 2007).

Due to the strong affinity of Hg^{2+} for S ligands, the cytotoxicity of Hg^{2+} is believed to be associated with its binding to -SH groups in functional proteins (Chen *et al.,* 2012) . Hg disrupts proteins involved in key cellular processes by altering cell membrane permeability and replacing essential metal ions with high affinity for -SH groups, which in turn may lead to protein precipitation (Patra *et al.,* 2004). Selenium plays a regulatory role in the stress response, sulfur metabolism, GSH metabolism, DNA replication, the cell cycle, and energy and carbohydrate metabolism, indicating its protective function against Hg toxicity (Li *et al.,* 2018). In addition, selenium effectively affects ATPase synthesis by preserving membrane lipid integrity, regulating pH and Ca^{2+} homeostasis, and competing with heavy metals for ion channels to enter root cells. Consequently, the addition of Se_3O^{2-} increases the activity of root H^+ -ATPase and Ca^{2+}-ATPase, significantly alleviating heavy metal toxicity in rice (O. sativa) tissues (Lin *et al.,* 2012).

The mechanisms of selenium interaction with various heavy metals, focusing on how selenium forms complexes with specific heavy metal ions and enhances plant tolerance by regulating gene expression. Molecular genetic approaches were employed to uncover the genetic regulatory mechanisms of selenium in plant resistance to heavy metal stress, elucidating the relationships among selenium, genes related to heavy metal resistance, and their regulatory networks Fig. (45).

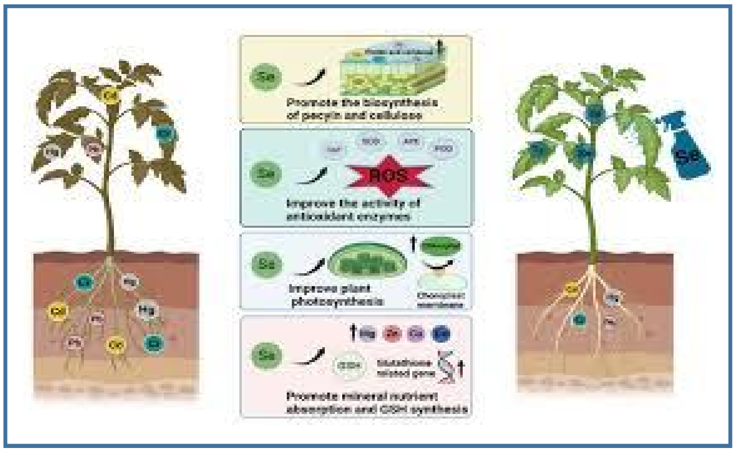


Fig. 45: Mechanism by which Se alleviates heavy metal stress in plants. After Yuan *et al.,* (2024)

Furthermore, the agricultural application potential of selenium was explored to assess its impact on crop yield and quality, as well as its practical effectiveness in remediating heavy-metal-contaminated soils. These in-depth investigations not only advance our understanding of mechanisms of selenium in alleviating heavy metal stress in plants but also provide scientific foundations for developing novel selenium remediation agents and strategies to enhance crops' heavy metal tolerance. These efforts aim to offer innovative solutions for addressing heavy metal pollution in modern agriculture and environmental conservation, thereby promoting sustainable agricultural development and improving environmental quality

Ulhassan *et al.* (2019) tested that effect of 5 and 10µM of Selenium supplementation on 100 and 200µM of Cr in B. napus. The authors noted a decline in major (N, P, K) and micronutrients (Zn, Fe, Mn) uptake under Cr stress. Application of Selenium (5 and 10µM) notably improved the mineral transportation under Cr contamination condition that was restricted in only stress condition (Ulhassan *et al.,* 2019). Apolonia *et al.* (2021) reported that purpose agronomic practices are one of the reasons for the increasing accumulation of elements in the soil, including manganese (Mn). Selenium ions can reduce the toxic actions of metal stress. Those, we studied the effects of Mn treated as a stressor and Selenium as a potential defense in plants. Methods Mn ions (10 mM) or/and Se (15µM) were added into hydroponic nutrients of two wheat cultivars. The evaluation of th Selenium stress-generating and protective actions were analyzed by biochemical methods and microscopic observations in leaves and roots. Moreover, the level of DNA methylation for these tissues was determined. Results Mn application caused an increase of lipid peroxidation and hydrogen peroxide content in both leaves and roots and was accompanied with a greater absorption of this element by the roots. For other elements (K, Fe, S, P), with the exception of Ca, the reduced their uptake was registered, especially in roots. Mn stimulated greater, microscopically observed, disorganization in cell structure particularly in roots as compared to leaves, which was accompanied by a quantitative increase in 5-methylcytosine (5-metC) in root meristem.

Selenium application diminished the effects of Mn-stress. Mn uptake led to drastic anatomical changes in cv. Nimfa roots (Fig. 46-C). These changes were often accompanied by degeneration of major growth apexes. In such roots, numerous cap cells were damaged and the meristematic cells were of abnormal shapes without visible nuclei (Fig. 46-C). Additionally, a characteristic group of compact, small cells with large nuclei at the meristem differentiation border was found (Fig. 46-C), which was not observed, in the control roots. When Mn was provided together with Se, the anatomy of the root growth apex in cv. Alibi (Fig. 46-D) and cv. Nimfa (Fig. 40-E) was more similar to the control, and there were no distinguished groups of cells above the meristem. In cv. Alibi, the meristematic cells were of correct shape (Fig. 46-D'), whereas irregularly shaped cells but with visible nuclei were still present in cv. Nimfa (Fig. 46-E'). In the roots a similar pattern of 5-metC localization (Fig.46- 5.I.A—C) and levels (Fig.46- 6A and B) was observed in the plants grown under control conditions. A very weak signal was localized in the meristematic and cap cells (Fig.46- 5.I.A). A successive increase in 5-metC was found in the nuclei of cells that entered the differentiation and elongation pathway (Figs.46- 5.I.B and C, 6A and B). In the root elongation zone, the strongest signal was detected in the nuclei of the cells of the differentiating vascular cylinder (Fig.46- 5.I.C). No signal was localized in control material, incubated without anti-5-metC antibodies (data not shown).

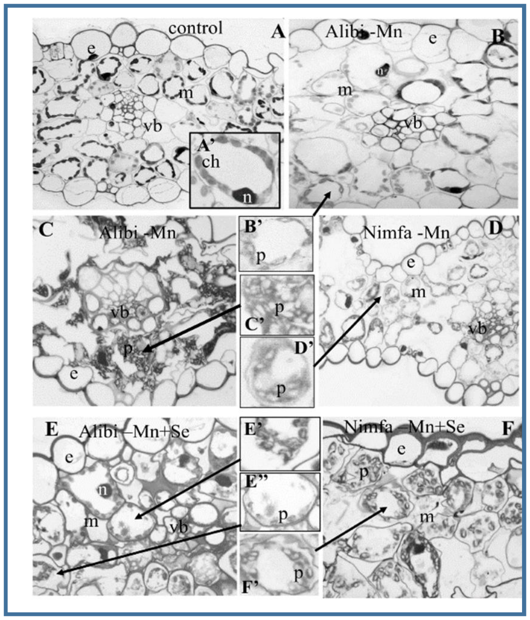


Fig. 46: Illustrates micrographs of sections of wheat leaves grown under control conditions and after treatment with 10 mM MnCl2 and 10 mM MnCl2+15 µM SeCl2. (e) Epiderm, (m) mesophyll cells, (vb) vascular bundle, (ch) chloroplast, (p) plastid, (n) nucleus. After Apolonia *et al.,* (2021)

They also reported that in the roots of cv. Alibi grown in the presence of Mn the increase in DNA methylation was observed from the differentiation zone to cell elongation zone, similarly as in control (Figs.46- 5. II. A-C and 6A). In the cap and meristematic cells, DNA was only slightly more methylated than in control (Fig.46- 6A). However, the tissues exhibiting anatomical abnormalities (Fig. 47). Showed also changes in their DNA methylation pattern. In the cap zone, the enhanced signal was visible only in single cells (Fig.47- 5.II. A), while the group of oval-shaped cells, not present in control (Fig. 47 B'), showed lower level of 5-metC than the surrounding cells (Figs.47 - 5.II.B, 6A – "different cells"). The elevated level of 5-metC was detected only in the cells on the procambium-procortex border (Fig.47- 5.II.B). In the elongation zone, the cells were irregular, some with no visible nuclei, and some with nuclei with a strong 5-metC signal (Fig.47- 5.II.C). Mn uptake leading to anatomical changes in cv. Nimfa roots (Fig. 47) was also reflected in 5-metC signal intensity in the nuclei (Figs. 47- 5.III.A—C, 6B). A signifcantly stronger signal was detected in the damaged cells of the root apex, i.e., the cap cells with irregular shapes and deformed nuclei and single meristematic cells with nuclei still present (Fig.47- 5.III.A). Additionally, higher level of 5-metC was found in the specifc group of small cells with highly condensed DNA (Fig. 47- 4C') on the meristem – differentiation zone border (Figs.47- 5.III.B, 6B – "different cells").

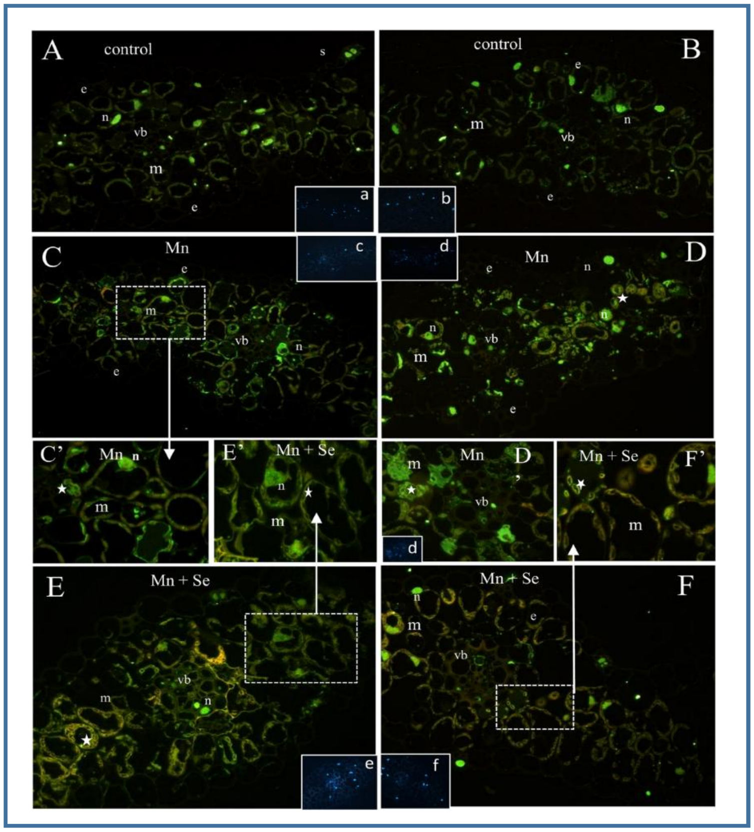


Fig. 47: Illustrates metC localization in Alibi (Fig. A, C, E) and Nimfa (Fig. B, D, F) leaves; a-f DAPI. (vb) vascular bundle, (m) mesophyll cell, (e) epidermis, (n) nucleus, (asterisx) plastid)×400. In the control plants (A, B) and those cultured in the presence of Mn (C, D) and Mn+Se (E, F) a similar signal was localized in the nuclei of leaves cells. Control in both cultivars' chloroplasts did not show autofuorescence (A, B). In the Mn media (C', D') and Mn+Se media (E', F') autofuorescence of plastids membranes was observed. After Apolonia *et al.,* (2021)

The above-discussed studies demonstrates the positive impact of Selenium application on ion homeostasis under heavy metals stress. However, more research is needed to unveil the mechanisms involved in Selenium induced maintaining of ions homeostasis in plants.

3- Conclusions and perspective

Metal toxicity is not only harmful for plant growth, development, and yield but also a threat for human health as metal enters the human body via the food chain. Therefore, consequences of heavy metal stress to agriculture and environment are very alarming and hence demands great attention to search and develop approaches for plant tolerance. Currently, exogenous Selenium application has been implemented as a remedial strategy for managing metal toxicity because of its beneficial functions. Selenium induced mechanisms in inhibiting the metal stress in plant, including reduction of metal uptake, and translocation to aerial parts, redistribution of subcellular metal distribution such as chelation and compartmentalization, improvement in plant nutrition as well as recovering photosynthesis and maintenance of osmoregulation. Upon exposure to metal stress, Selenium induced the upregulation of antioxidants responses, lowering ROS generation in plant along with strengthening of cell membrane stability. Using of Selenium for increasing yield under metal contamination has been also demonstrated, which resulted in better production in plants and thus provides new hope to increase food production under the threat of heavy metals.

Toxicity of heavy metals to plants and their mechanisms by which plants detoxify heavy metals are currently important. Heavy metals disrupt normal cellular metabolism and cause damage to plant structures, thus affecting plant growth and development. Selenium assists in improving plant antioxidant systems, repairing damaged cell structures and functions, and promoting the formation of selenium-heavy metal complexes and metallothionein. In recent years, many nations have adopted the application of selenium and biofortification techniques to reduce abiotic stress and produce selenium-enriched food. However, further in-depth knowledge of selenium metabolism, signaling, and seleno-compound activities in plants is required to achieve its desired effects. Additionally, research on nano conjugates containing SeNP may have the way for improving positive impacts on plants. Abiotic stresses are abiotic environmental conditions that are not conducive to plant survival, growth, and development and even lead to injury, destruction, and death. Selenium can reduce the harmful effects of abiotic stresses on plants. This study describes the transportation and metabolism of selenium in plants and summarizes the mechanisms by which selenium alleviates abiotic stress in plants through:

- The photosynthetic properties of plants, which promoting the synthesis of photosynthetic pigments and repair the damage of photosynthetic organelles, such as chloroplasts in plants.
- The activities of antioxidant enzymes, selenium can significantly enhance the activities of antioxidant enzymes, such as SOD, POD, and CAT, and accelerate the removal of excessive ROS in plants.
- Regulates cell permeability and promotes the accumulation of resistant substances, selenium can promote the content of osmoprotectants, such as proline and soluble sugar, thus maintaining cell osmotic pressure.
- Inhibits the transport of salt and metal ions in plants, selenium can encourage these ions to form complexes or precipitate, effectively reducing their uptake in plants.
- Regulates the expression of related genes and proteins to improve plant tolerance.

Further investigations are needed to reveal the molecular mechanisms by which selenium regulates abiotic stress response in plants. Some advanced technologies, such as the genomics, transcriptomics, and proteomics, can help identify the key genes, metabolites, proteins, and regulators that play key roles in the regulation of selenium on abiotic stress. Applying suitable concentrations of Selenium in crops may be a selectable way to mitigate crop losses in the presence of abiotic stress. However, the application of selenium needs caution because inappropriate concentrations of selenium may exert toxic effects on plants

Research must also be executed from a safety viewpoint, as broad scale Selenium application in agriculture sector, especially at high concentration, may cause toxicity in plants and animals or even higher intake of Se may induce diseases in humans. In addition, the interactive effects of Se to other metabolites, plant nutrients, hormone, and signaling molecules should be emphasized by in-depth studies for getting best approaches in increasing plant tolerance to metal toxicity with the reduction of residual effects in food crops. However, in-depth studies considering Se-induced mechanisms in plant at molecular and physiological levels need to be investigated further in field condition for economically important plant species.

Acknologment

We extend our heartfelt condolences to Professor Mohamed Abou Seeda, the main author of this paper, who sadly passed away on April 19, 2025. His contributions to the field were substantial, and his passion for research will be deeply missed by colleagues and students alike. We honor his legacy by continuing to support the pursuit of knowledge he valued so highly.

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