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Toxicity of Silver Nano Particuls, Molecular Reaction and Their Tolerance in Plants: A Review

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ABSTRACT

Uptake of AgNPs by plants depends on the size and shape as well as the exposure concentration of AgNPs, but mechanisms of AgNPs internalization and distribution in plants are not fully understood. Their impact on morphological and physiological features of plants depends on AgNP characteristics, transformation possibilities as well as on the plant species and developmental stage and the way of exposure. Roots are the first tissue to be in contact with AgNP solution, toxic symptoms appear more frequently in roots than in shoots, although AgNPs also induce morphological modifications in the stem and leaves. The main subcellular targets affected by AgNPs are mitochondria, nucleus and in particular chloroplasts, which is in line with detrimental impact of AgNPs on the structure and function of the photosynthetic apparatus. Moreover, damaged chloroplasts contribute to ROS generation and oxidative stress has an important role in the phytotoxicity of AgNPs. However, the underlying mechanisms of AgNP-mediated ROS production need further investigations. Proteomic analyses indicate that AgNPs predominantly affect proteins related to cell metabolism, stress response and signaling. The question whether phytotoxic effect is specific for nanoparticles or it is the result of the action of Ag^+ released from AgNPs in exposure solution and/or after biotransformation in the cellular structures remains unresolved.

Keywords: uptake, mechanisms, silver, nano Particuls, toxicity, morphological and physiological, Tolerance.

1. Introduction

Continuous formation, production and utilization of nanoparticles and their unregulated release into aquatic as well as terrestrial systems via number of pathways, have resulted in a growing concern over their impending environmental effects Ray *et al.,* (2009), Smita *et al.,* (2012). Among different available NPs, silver nanoparticles (AgNPs) are of particular interest because of their well-known antibacterial and antifungal properties due to which they have been implemented in a wide range of commercial products such as medical devices, textiles, food packaging, and healthcare and household products Ahamed *et al.,* (2010), Tolaymat *et al.,* (2010). AgNPs are known to induce toxicity in prokaryotic Suresh *et al.,* (2010), eukaryotic Ahamed *et al.,* (2010) and aquatic Fabrega as well as in in vitro systems Foldbjerg *et al.,* (2011). The (cyto) toxicity of AgNPs has been attributed to several possible mechanisms, including disruption of cell-membrane integrity Suresh *et al.,* (2010), protein or DNA binding and damage Arora *et al.,* (2009), reactive oxygen species (ROS) generation Hsin *et al.,* (2008) as well as apoptotic cell death Gopinath *et al.,* (2010). However, it is still not clear to which degree the toxicity of AgNPs results from AgNPs and how much toxicity is related to the released Ag^+ Navarro *et al.,* (2008), Kawata *et al.,* (2009). AgNPs are prone to various environmental (bio)

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transformations, which modify their properties influencing their transport, fate and possible toxicity Reidy *et al.,* (2013), proper characterization of AgNPs as well as direct detection and localizations within plant tissues are indispensable to reveal direct interaction of silver nanoparticles with plants. Plants are the vital part of ecosystems as primary producers and they play a significant role in accumulation and bio distribution of many environmentally released substances. They are very likely to be influenced by AgNPs, serving as a potential pathway for AgNP-transport and bioaccumulation into food chains Rico *et al.,* (2011). Therefore, any negative effects of NPs upon plant growth could cause significant changes in the ecosystem, potentially causing irreversible damage. AgNPs can adversely affect plants indirectly, via AgNP containing products for human usage that are being released to the environment Luoma (2008). Moreover, they can also be directly exposed to AgNPs through application of the commercially available products that are being implemented in agriculture, since nanotechnology has been applied in plant production to increase plant growth Sekhon (2014) and to improve pest and disease management Servin *et al.,* (2015), Pallavi *et al.,* (2016). Tripathi *et al.,* (2017), Verma *et al.,* (2018). Several researchers reported that the toxicological studies of AgNPs conducted on plants depending on various factors regulating the uptake and accumulation such as plant species and age, the nanoparticle size and concentration, as well as on the test conditions i.e. temperature, duration and method of exposure El-Temsah *et al.,* (2012), Yin *et al.,* (2012). Recently published studies which focused on plant uptake and accumulation of AgNPs and their effects on different aspects of plant physiology, such as germination, growth and plant morphology and as well as photosynthesis Fig. (1) .Moreover, roles of AgNP in promotion of oxidative stress, followed by responsive plant antioxidant machinery, as well as in changes in protein expression, which require further research to understand the molecular response triggered by AgNPs in plants.

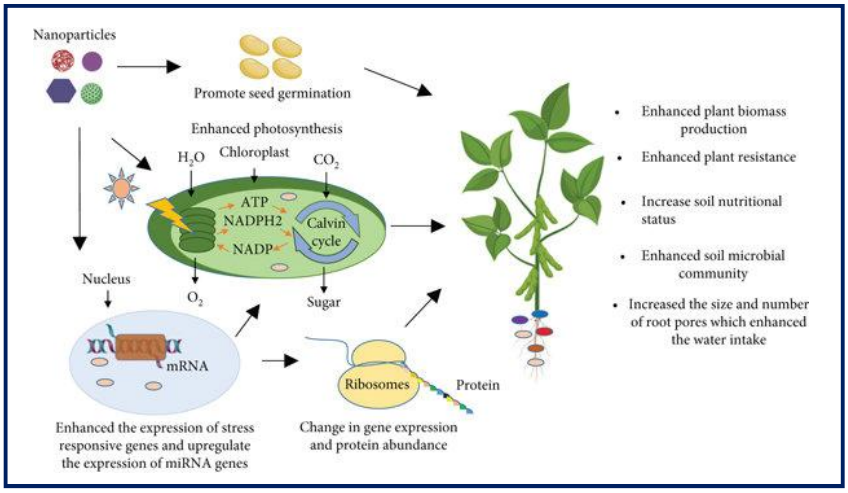

Fig. 1: Illustrates positive effects of nanoparticles on plant growth and development. The optimum concentration of nanoparticles causes an alteration in different physiological processes to increase seed germination and photosynthesis of the plants. Further, the nanoparticles alter the gene expression of different genes and miRNAs that have a positive impact on stress tolerance and plant biomass. After Shahid *et al.,* (2021)

Shahid *et al.,* (2021) reported that photosynthesis is the essential mechanism that converts light energy to chemical energy for plants on earth. All living things rely on photosynthesis either directly as their energy source or indirectly as their food's ultimate energy resource. In chloroplasts, the light source of energy is converted into a chemical form using chlorophyll, H_2O, and CO_2 as raw materials and stored in sugar molecule bonds. Several studies reported that foliar application of metal NPs dramatically improves the content of chlorophyll in plants, enabling plants to synthesize more complexes for light harvesting to absorb more light energy and improve photosynthesis. TiO_2 is the most studied NP because it has a photo catalytic quality and can activate an oxidation-reduction reaction, contributing to the charge transfer between light-harvesting complexes II and TiO_2 NPs Kuang

et al., (2003). The effect of TiO_2 NPs on the photosynthetic efficiency of spinach has been reported, indicating that TiO_2 NPs can increase light absorption and accelerate light energy transport and transformation. Furthermore, due to the delay in the successful photosynthetic tenure of chloroplasts, TiO_2 NPs will prevent chloroplasts from aging. Nanoanatase TiO_2 enormously improved the electron transport chain, O_2-evolving and photophosphorylation activity, and PSII photo reduction function of chlorophyll in spinach under both visible and ultraviolet (UV) radiation Lei *et al.,* (2007). In addition, the soluble protein and chlorophyll content of the ZnO NP-treated plants increased by 25% and 34.5%, respectively, compared to those of the control Raliya *et al.,* (2016). Chlorophyll content increased from 62.67 to 227.42% with an aerosol-foliar spray with rising concentrations of TiO_2 NPs up to 500 mg kg1. The transfer of TiO_2 NPs in soil induces a maximum increase in chlorophyll content of 216.29% at a concentration of 750 mg kg^{-1} Raliya *et al.,* (2015). In A. thaliana, TiO_2 NP-treated plants have 3.83 times greater light-harvesting complex II (LHCII) content as compared to the control. Fig. (2).

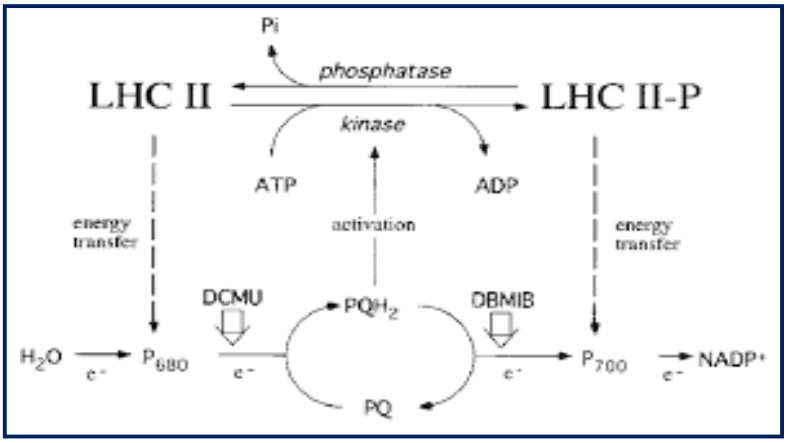

Fig. 2: Illustrates distribution of LHC II between Photosystems I and II by redox-activation of its protein kinase. After Allen (1992)

Silver technophility has been growing at an exponential rate and, according to forecasts, will only increase soon Kasimov and Vlasov (2012). The main anthropogenic sources of silver pollution of the environment, including soils, are emissions from thermal power plants during coal combustion Nriagu and Pacyna (1988) , Krylov (2012), nonferrous and ferrous metallurgy enterprises Medvedskaya (2009), cement plants Pashkevich and Alekseenko (2015) solid waste landfills Sherbakova.(2013), production of photo and electrical materials Eisler (1996), pesticides Stampoulis, *et al.,* (2009), the use of sewage sludge as fertilizers Michels, *et al.,* (2017).The extent and degree of silver pollution in soils are increasing every year Auevirivavit, *et al.,* (2014), Benn, *et al.,* (2010).

In modern conditions of nanotechnology development, silver nanoparticles are increasing sources of environmental pollution Pal, *et al.,* (2007), Eivazi, *et al.,* (2018). Silver toxicity has been established for bacteria Gogoi, *et al.,* (2006), Singh, *et al.,* (2018), plants Sillen, *et al.,* (2015), Tripathi, *et al.,* (2017), Galazzi and Arruda (2018) , nematodes Yang, *et al.,* (2017), earthworms Das, *et al.,* (2018), mollusks Liu, *et al.,* (2018), fish Sayed and Soliman (2017), Abramenko, *et al.,* (2018), rats Hussain, *et al.,* (2005), Sun, *et al.,* (2016), mice Jiravova, *et al.,* (2016) and human Gaillet and Rouanet (2015), Hadrup *et al.,* (2018). Silver ions Ag^+ possess genotoxic properties Butler, *et al.,* (2015), Guo, *et al.,* (2016). Silver is capable of interacting with various proteins Cao and Liu (2010), Gomathi *et al.,* (2017). Therefore, the mechanism of silver toxicity is apparently the same as that of other heavy metals and metalloids inhibition of enzymes and a decrease in the permeability of biological membranes Michels, *et al.,* (2017), Hussain, *et al.,* (2005) Sun, *et al.,* (2016), DNA damage Sayed and Soliman (2017), Sharma, *et al.,* (2014), metabolic disturbance Liu, *et al.,* (2018), Gomathi *et al.,* (2017), Sharma, *et al.,* (2014), and cell necrosis Sun, *et al.,* (2016). At the same time, the environmental effects of silver soil pollution have been studied to a much lesser extent than those of other heavy metals such as lead, cadmium, and mercury. Therefore, it seems relevant to identify patterns of the effect of silver on the state of soils depending on the dose of metal and the period from the moment of contamination, to

establish limits on the resistance of different soils to pollution, and to normalize the silver content in soils. The aim of this work is to assess the eco-toxicity of silver by biological indicators of soil condition, which differ significantly in the degree of resistance to pollution.

Silver toxicity depends on the concentration of active free silver ions (Ag^+), found primarily in the aqueous stage. Several processes in medium and water characteristics reduce silver toxicity by preventing free Ag^+ formation or by avoiding binding Ag^+ to organisms ' reactive surfaces. For a long time, the toxic effects of Ag on plants grown on the ground have not been reported Khanna *et al., (*2018). Ratte (1999) reported that about 5 mg/Kg Ag in shoots and about 1500 mg/Kg in bush bean roots significantly reduced yields without any symptoms of toxicity Wallace *et al.,* (1977) reported that Ag in the nutrient medium at a very low concentration (10 µg/L) stimulated the growth of grass roots. He speculated that some cations (e.g., Ag, Co, and Cu) could indirectly change cell metabolism, leading to a higher cell growth rate. The Ag replaces K^+ sites in membranes and prevents the roots from absorbing other cations. High Ag concentrations (up to 1 µM/L) significantly decrease growth and protein content, while sunflower enzyme urease activity is increased Krizkova *et al.,* (2008).

1- Mobility of AgNPs in soils

There is growing evidence that AgNPs released into the different types of environment including soil, water and air from where they could be taken and accumulated in plants. Studies of AgNP-induced phytotoxic effects conducted on different plant species reported contradictory results, showing that impacts of AgNPs on plants largely depend on the type and concentration of nanoparticles, plants species, tissue exposed, and the experimental conditions Ma *et al.,* (2010), Ma etal., (2018). Various types of AgNPs can exhibit distinct characteristics depending on their size, charge and surface properties, which can influence their behavior, uptake as well as toxicity Yin *et al.,* (2011), Levard *et al.,* (2012) Fig.(3) Exposure to smaller particles with larger surface areas in higher cellular uptake and toxic responses Geisler-Lee *et al.,* (2013), Wang *et al.,* (2013). In addition, different characteristics of the media used for plant growth such as (pH, ionic strength, redox conditions) could modify initial properties of synthetized AgNPs and consequently influence their bioavailability, bioaccumulation as well as biological effects.

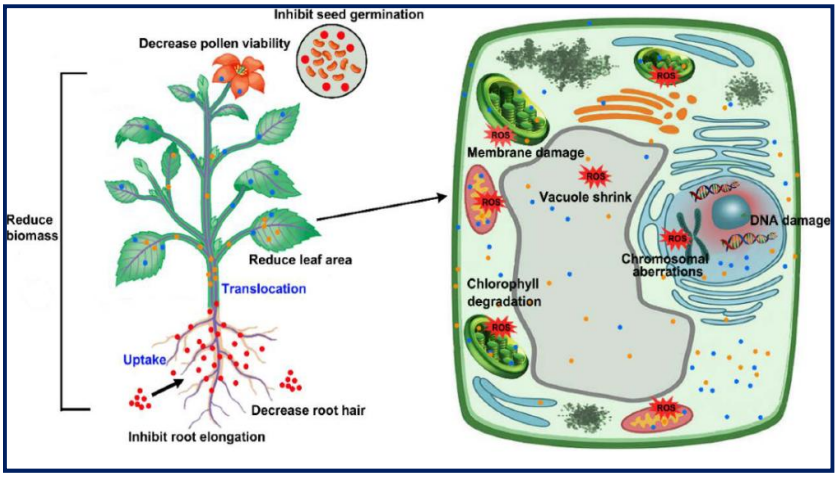

Fig. 3: Diagram representing uptake, translocation, and major phytotoxicity of silver nanoparticles (AgNPs) in plant Yan and Chen (2018). Generally, AgNPs are taken up by underground tissues (primary roots and lateral roots), then translocated to aboveground parts (stem, leaf, flower, etc.), where they can reduce biomass, decrease leaf area, affect pollen viability, and inhibit seed germination. At the cellular level, AgNPs enter into various organelles, leading to the production of excess reactive oxygen species (ROS), thereby causing cytotoxicity and genotoxicity, such as membrane damage, chlorophyll degradation, vacuole shrinkage, DNA damage, and chromosomal aberrations.

Regarding the fate of AgNPs and their behavior come from investigations in aquatic systems and several reports pointed out differences in AgNPs behavior in deionized water used for preparation of

stock solution and various media used for exposure Reidy *et al.,* (2013). Environmental transformations of AgNPs show that slow oxidative dissolution by molecular oxygen and protons, reactions with reduced sulphur species or chloride, adsorption of polymers, natural organic matter or proteins, and aggregation that depends on media and coatings, Behra *et al.,* (2013), Levard *et al.,* (2012), and Sharma *et al.,* (2014). Most important processes for the bioavailability of AgNPs and their biological effects include agglomeration or aggregation of NPs to form larger particles, oxidation of elemental silver (Ag^0) to silver ion (Ag^+) and subsequent dissolution to dissolved Ag^+ species, speciation and solubility of Ag^+ in solution and reactions modifying the reactivity of AgNPs Behra *et al.,* (2013). The presence of ions in the medium will effectively destabilize the AgNPs, leading to aggregation Levard *et al.,* (2012), Thwala *et al.,* (2013). Agglomeration can reduce the mobility and modify the initial concentration of AgNPs thus, influencing their toxic effects Barrena *et al.,* (2009), Miao *et al.,* (2010). To stabilize AgNPs against aggregation, different coating are applied including carboxylic acids (citrate), polymers (poly vinyl pyrrolidone, PVP), polysaccharides (gum Arabic, GA), and surfactants (cetyl trimethyl ammonium bromide, CTAB and sodium dodecyl sulfate, SDS). Which change the surfaces of AgNPs and thus, affect their behavior and transformations in the medium Levard *et al.,* (2012) as well as their toxicity to plants Yin *et al.,* (2011), Cvjetko *et al.,* (2017), Zou *et al.,* (2017). Fig. (4).

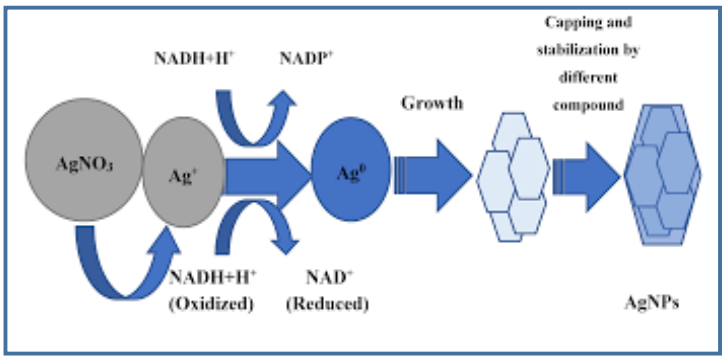

Fig. 4: Uptake of differently coated and uncoated AgNPs in plants and freshwater algae and their effects on growth and morphology. EPS extracellular polymeric substances.

Aerobic conditions result in the oxidation of AgNPs and release of Ag^+, creating a major role in toxicity .Fig. (5).

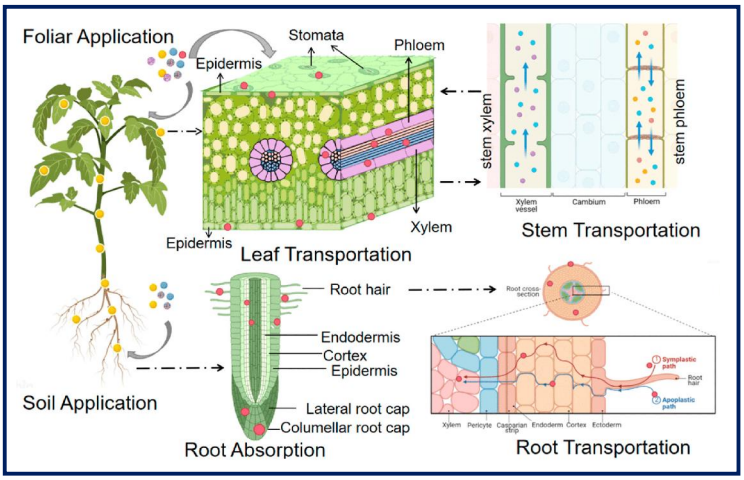

Fig.5: Illustrates a schematic diagram of the uptake and translocation of NPs in plants through foliar application or root exposure treatment. After Wang *et al.,* (2023)

Dissolution rate is influenced by the pH and the presence of strong binding ligands, which can be very different in the various types of media, used for plant growth Behra *et al.,* (2013). Chlorides (Cl^{-1}) in exposure solution would result in formation of AgCl, thus removing free Ag^{+} Dimkpa *et al.,* (2012) Sulfidation i.e. formation of Ag_2S is also possible, which can limit AgNPs bioavailability and toxicity Lowry *et al.,* (2012). On the other hand, AgNP transformation in the soil and other solid media has been poorly analysed Coutris *et al.,* (2012), Anjum *et al.,* (2013), due to the lack of adequate techniques. That surface reactive particles, such as clays and organic matter-coated particles present in soil, can affect the behavior of AgNPs, favouring their aggregation and thus, decreasing the risk of toxicity Lee *et al.,* (2012), Yin *et al.,* (2011) Dimkpa *et al.,* (2012), Anjum *et al.,* (2013).

2- Translocation of AgNPs in Plants

Silver nanoparticles (AgNPs) are transported through the intercellular spaces (short-distance transport) and through vascular tissue (long-distance transport) Ma *et al.,* (2010), Geisler-Lee *et al.,* (2013), Miralles *et al.,* (2012) Fig. (6). These recent findings shed light on an advanced concept that the xylem and the phloem pathways develop a long-distance root-to-shoot and then shoot-to-root signaling feedback circuit in plants. Signal molecules are transmitted across long-distances to response the soil environments via the vascular tissues with the following sequential processes. First, the information signaling molecules, generated in somewhere or in all parts of the branched root system, move shoot-ward via the xylem. Second, the signals run through a stem region between branched root and branched shoot and disperse to each of the mature leaves, possibly to the minor veins Fig. (6- 1A). Third, the signal molecules are translocated from the xylem to the phloem and perceived by the receptors located on the phloem cells. In this process, the information is converted to the secondary signal inside of the phloem cells Fig. (6- 1B).

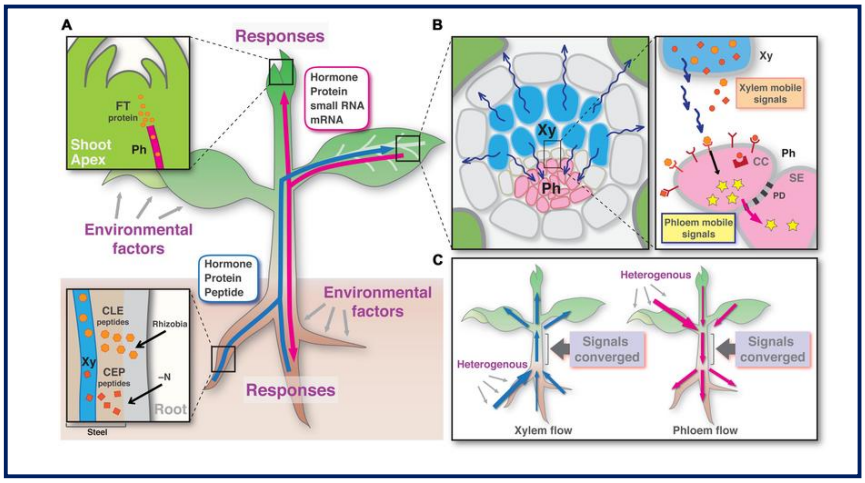

Fig. 6: A model of long-distance signaling via plant vascular tissues. (A) Potential signal molecules of the xylem (blue) and the phloem (red) translocation pathways. Insets show xylem loading and phloem unloading of signal molecules in the sink tissues. (B) Signal relay from the xylem to the phloem in the leaf vein. (C) Signal convergence by running through a stem region in each of xylem and phloem pathways. Xy, xylem; Ph, phloem; CC, companion cell; SE, sieve element; PD, plasmodesmata. After Notaguchi and kamoto (2015)

Fourth, the intracellular signal molecules travel on the phloem sap flow, including shoot-to-root translocation. Thus, finally the information signals generated in a part of root system can transmit to another part of the root. In each of these shoot- and root ward translocation flows, all signaling molecules generated in branches of organs in response to heterologous environmental factors should be physically converged by running through a stem region (the bases of shoot and root), which ought to be the sole pathway Fig.(6-1C).

After exposure to plants, NPs penetrate cell walls and plasma membranes of epidermal layers in roots, followed by a series of events to enter plant vascular tissues (xylem), and move to the stele. Xylem is

the most important vehicle in the distribution and translocation of NPs Aslani *et al.,* (2014). Through xylem, AgNPs can be taken up and translocated to leaves. In *Arabidopsis thaliana*, AgNPs can be taken up by the roots and transported to the shoots Ma *et al.,* (2010). Geisler-Lee *et al.,* (2013) found that AgNPs was taken up and progressively accumulated in the root tips, from border cells to root cap, epidermis, columella, and initials of the root meristem. A further study indicated that AgNPs attached to the surface of primary roots in *Arabidopsis* and then entered root tips at an early stage after exposure. After 14 days, AgNPs gradually moved into roots and entered lateral root primordia and root hairs Fig. (7).

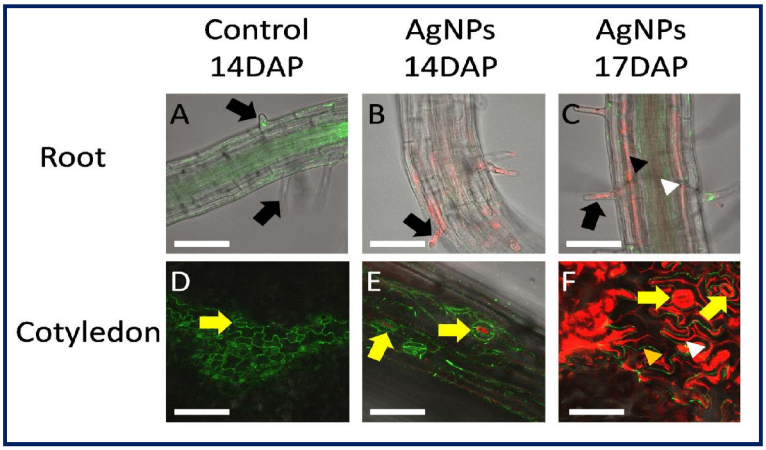

Fig. 7: Illustrates Silver Accumulation in Plant Tissues and Remainder in Soil. After Geisler-Lee *et al.,* (2014)

After multiple lateral roots were developed, AgNPs were present in vascular tissue and throughout the whole plant from root to shoot Geisler-Lee *et al.,* (2014). The cell wall of the root cells is the main site through which AgNPs enter in plant cells Tripathi *et al.,* (2017). In order to enter into the plant, AgNPs need to penetrate the cell wall and plasma membranes of epidermal layer of roots. The cell wall is a porous network of polysaccharide fiber matrices and, thus, acts as natural sieve Navarro *et al.,* (2008), Carpita, and Gibeaut (1993). The small-sized AgNPs can pass through the pores, whereas larger AgNPs are unable to enter into plant cells and are thereby sieved out Tripathi *et al.,* (2017). Interestingly, AgNPs can induce the formation of new and large-sized pores, which permits the internalization of large AgNPs through the cell wall Navarro *et al.,* (2008). AgNPs can also be transported within the plant cell through the plasmodesmata process Ma *et al.,* (2010), Heinlein and Epel (2004), Lucas, and Lee, (2004). Plasmodesmata are pores of 50–60 nm in diameter and connect adjacent neighboring plant cells. In *Arabidopsis*, AgNPs are found to aggregate in plasmodesmata and in the cell wall Geisler-Lee *et al.,* (2013), suggested that there may be blockage of intercellular communication, which may be caused by the mechanical presence of AgNPs at these sites and may affect nutrient intercellular transport Geisler-Lee *et al.,* (2014). In addition to the root pathway, AgNPs can also be taken up through plant leaves. Geisler-Lee *et al.,* (2014) found that if cotyledons of the *Arabidopsis* seedlings were immersed in AgNP-containing medium, AgNPs could be taken up and accumulated in stomatal guard cells Geisler-Lee *et al.,* (2014). Larue *et al.,* found that AgNPs were effectively trapped on lettuce leaves by the cuticle after foliar exposure, and AgNPs could penetrate the leaf tissue through stomata Larue *et al.,* (2014). In addition, uptake of AgNPs by soybean and rice following root versus foliar exposure, and found that foliar exposure resulted in 17–200 times more Ag bioaccumulation than root exposure Li *et al.,* (2017). Once the AgNPs enter into vascular tissues of crops, they can be taken up and transported to the leaves or other organs through long-distance transport Dietz and Herth (2011), Ma *et al.,* (2010), Geisler-Lee *et al.,* (2014). Therefore, AgNPs may also subject the fruits, seeds, and other edible parts of plants to contamination through translocation.

3. Factors affecting nanoparticles

3.1. Impacts on plant uptake

Nanoparticles uptake by plant is affected by several factors related to the nature of the nanoparticle itself, but also with the plant physiology and the interaction of the nanomaterials with the environment Fig. (8). It is clear that nanoparticle traits will greatly influence its behavior, and hence if the plant will be able to absorb it. Size seems to be one of the main restrictions for penetration into plant tissues, and there are some reports about the maximum dimensions that plants allow for nanoparticles to move and accumulate inside the cells, usually with 40–50 nm as a size exclusion limit González-Melendi *et al.,* (2008); Corredor *et al.,* (2009); Sabo-Attwood *et al.,* (2012); Taylor *et al.,* (2014).

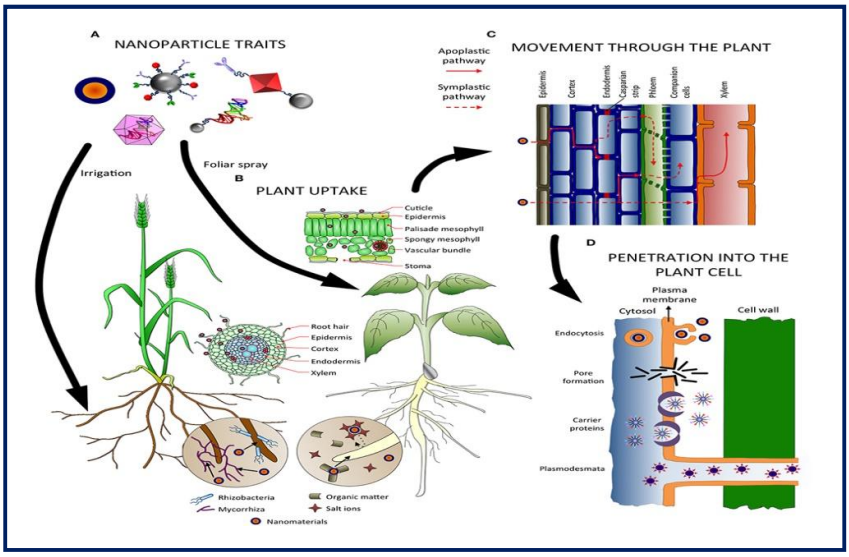

Fig. 8: Factors influencing absorption, uptake, transport and penetration of nanoparticles in plants. (**A**) Nanoparticle traits affect how they are uptaken and translocated in the plant, as well as the application method. (**B**) In the soil, nanoparticles can interact with microorganisms and compounds, which might facilitate or hamper their absorption. Several tissues (epidermis, endodermis...) and barriers (Casparian strip, cuticle...) must be crossed before reaching the vascular tissues, depending on the entry point (roots or leaves). (**C**) Nanomaterials can follow the apoplastic and/or the symplastic pathways for moving up and down the plant, and radial movement for changing from one pathway to the other. (**D**) Several mechanisms have been proposed for the internalization of nanoparticles inside the cells, such as endocytosis, pore formation, mediated by carrier proteins, and through plasmodesmata. After Alejandro Pérez-de-Luque. (2017)

Additionally, the type of nanoparticle and its chemical composition is another factor influencing the uptake Ma *et al.,* (2010); Rico *et al.,* (2011), whereas, morphology has also been demonstrated as determinant in some cases Raliya *et al.,* (2016). Functionalization and coating of the nanomaterial surface can greatly change and alter the properties for its absorption and accumulation by plant Judy *et al.,* (2012). Plant species can differ in their physiology, due to variations regarding uptake of nanoparticles, as reported Cifuentes *et al.,* (2010), Larue *et al.,* (2012), and Zhu *et al.,* (2012). These works showed how crops species belonging to different botanical families, and exposed to either magnetic carbon-coated, titanium dioxide or gold nanoparticles respectively, presented diverse absorption and accumulation patterns inside the plants. However, the ways of application are also crucial in order to determine how effectively a plant will internalize the nanomaterials: roots are specialized in absorption of nutrients and water, whereas leaves are developed for gas exchange and present a cuticle that hampers penetration of substances Schwab *et al.,* (2015). Nevertheless, nanoparticles interact with other components of the environment, and it can affect their properties and their traits for being assimilated by plants Fig. (8). Humic acids and other organic matter in the soil can improve stability and hence a better bioavailability of nanomaterials, whereas salt ions might induce

precipitation and trigger a contrary effect Navarro *et al.,* (2008). Even more, the presence of other organisms, such as bacteria and fungi, influences the plant uptake of nanoparticles, mainly if those microorganisms establish symbiosis with plants as in the case of mycorrhizal fungi Feng *et al.,* (2013); Wang *et al.,* (2016).

3.2. Interaction of Nanomaterials with Plant Cells

In order to enter the symplastic pathway, nanomaterials must be internalized by the plant cell and cross the plasma membrane. Several ways for nanoparticles to achieve this, although such mechanisms are better studied in animal cells and less known in plants Rico *et al.,* (2011); Schwab *et al.,* (2015), *Endocytosis:* The nanoparticles are incorporated into the cell by invagination of the plasma membrane, originating a vesicle that can travel to different compartments of the cell Etxeberria *et al.,* (2006). Pore formation: Some nanomaterials can disrupt the plasma membrane, inducing the formation of pores for crossing into the cell Wong *et al.,* (2016) and reaching directly the cytosol without being encapsulated in any organelle Serag *et al.,* (2011). Carrier proteins: Nanoparticles can bind to surrounding proteins, including cell membrane proteins that could act as carriers for internalization and uptake inside the cell Nel *et al.,* (2009). Specifically, aquaporin have been suggested as transporters for nanomaterials inside the cell Rico *et al.,* (2011), but their tiny pore size, ranging between 2.8 and 3.4 Å Wu and Beitz, (2007), makes them unlikely as channels for nanoparticle penetration Schwab *et al.,* (2015), unless such pore size could be modified and increased. *Plasmodesmata:* Another way for nanomaterials entering a cell is through plasmodesmata, specialized structures for transport between cells Roberts and Oparka, (2003). Of course, it involves that the nanomaterials should be already in the symplast, but this mechanism is important in plants for translocation through the phloem Zhai *et al.,* (2014). *Ion channels:* They have been proposed as probable pathways for nanoparticles entry into the cell Rico *et al.,* (2011), Schwab *et al.,* (2015). However, the size of such channels is around 1 nm, which makes very unlikely for nanoparticles to effectively cross them without important modifications. How nanoparticles are internalized in the cells is another key question, because it will again influence the practical application of the nanomaterials. If we want to deliver chemicals inside specific cell organelles, then endocytosis appears as the most suitable way. On the contrary, for delivery in the cytosol, pore formation should be the most direct way for it. Additionally, we could be interested in nanomaterials that do not penetrate inside the plant cell but in other organisms, such as bacteria or fungi, to treat crop systemic diseases and infections Rispail *et al.,* (2014).

4. Phytotoxicity of AgNPs

4.1. Phytotoxicity at the Morphological Level

Several researchers, Dietz and Herth (2011), Aslani *et al.,* (2014), Tripathi *et al.,* (2017) reported that exposure to AgNPs, have significant changes in the morphology of plants. Growth potential, seed germination, biomass, and leaf surface area are the commonly used parameters for assessing the phytotoxicity of AgNPs in plants Fig. (9).

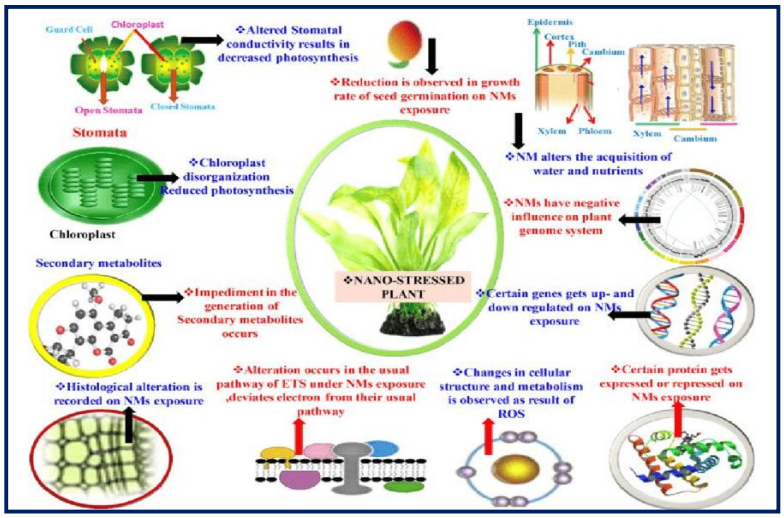

Fig. 9: Illustrates that phytotoxicity of nanoparticles at the cellular Level. After Tripathi *et al.,* (2017).

Exposure of AgNP could inhibit seed germination and root growth, and reduce biomass and leaf area. Jiang *et al.,* (2012) found that AgNPs significantly decreased plant biomass, inhibited shoot growth, and resulted in root abscission in *Spirodela polyrrhiza*. Kaveh *et al.,* (2013) showed that exposure to higher concentrations (from 5 to 20 mg/L) of AgNPs resulted in reduction of the biomass in *Arabidopsis* , Dimkpa *et al.,* (2013) found that AgNPs reduced the length of shoots and roots of wheat in a dose-dependent manner in wheat. Similarly, showed that AgNPs significantly reduced root elongation, and shoot and root fresh weights in rice plants. Stampoulis *et al.,* (2009) demonstrated that AgNPs (>100 mg/L) inhibited seed germination and reduced biomass in zucchini (*Cucurbita pepo*). Similar results regarding the toxicity on seed germination, biomass accumulation, and root and shoot growth by AgNPs were reported in other studies involving various plant species, including *Arabidopsis* Qian *et al.,* (2013) , *Brassica nigra* Amooaghaie *et al.,* (2015) , Lemna Gubbins *et al.,* (2011) , *Phaseolus radiatus* and *Sorghum bicolor* Lee *et al.,* (2012) , *Lolium multiflorum* Yin *et al.,* (2011) , rice Ejaz *et al.,* (2018) , wheat Yang *et al.,* (2018) , *Lupinus termis* L. Al-Huqail *et al.,* (2018). A summary of compiled descriptions of the effects of AgNPs in plants.

Seed germination represents the first and the most crucial step for plant growth and the overall crop yield Szollosi, *et al.,* (2020). It is the most sensitive stage of plant ontogenesis, heavily susceptible to various environmental factors, such as AgNP exposure, that can modulate metabolic processes during germination and ultimately affect plant growth Tymoszuk *et al.,* (2021) . To assess the effects of AgNP on seed germination and early growth, most of the conducted studies examined germination percentage and rate, root, and shoot elongation, plant morphology, and changes in biomass Tkalec *et al.,* (2019) , Biba *et al.,* (2020) , Biba etal (2021), Pacheco and Buzea (2017) . Results showed both positive and negative effects, depending on the plant species, exposure method, and characteristics of AgNPs (reviewed in Tkalec *et al.,* (2019).

Another important factor determining AgNP phytotoxic effects is their uptake. The main route of AgNPs entry into the plant cell occurs through the pores in the cell wall Tripathi *et al.,* (2017), Navarro *et al.,* (2008). Their further translocation occurs by endocytosis and through plasmodesmata Fabrega *et al.,* (2011), Ma, *et al.,* (2010). AgNP movement and effects are highly dependent on the plant growth stage. If taken up by roots of seedlings or adult plants, AgNPs can penetrate the vascular tissue and reach the stems and leaves Fig. (10), where they can cause further damage Navarro *et al.,* (2008). If AgNPs enter the seeds during imbibition period, they can move to embryonic cells and in that way cause long-term effects for the plant Prazak *et al.,* (2020). Mostly their size and surface coating that play an important role in AgNP uptake and modulate their effects on germination and development determine properties of AgNPs. Electrostatically stabilized citrate-coated AgNPs showed higher potential for medium induced modifications, consequently, leading to their pronounced phytotoxic effects. In a study by Pokhrel *et al.,* (2013), noticed that AgNP-citrate significantly inhibited seed germination of cabbage and maize, but the effects on root elongation were found to be species-dependent. AgNP-citrate had no effect on maize root growth, but it inhibited growth of cabbage roots.

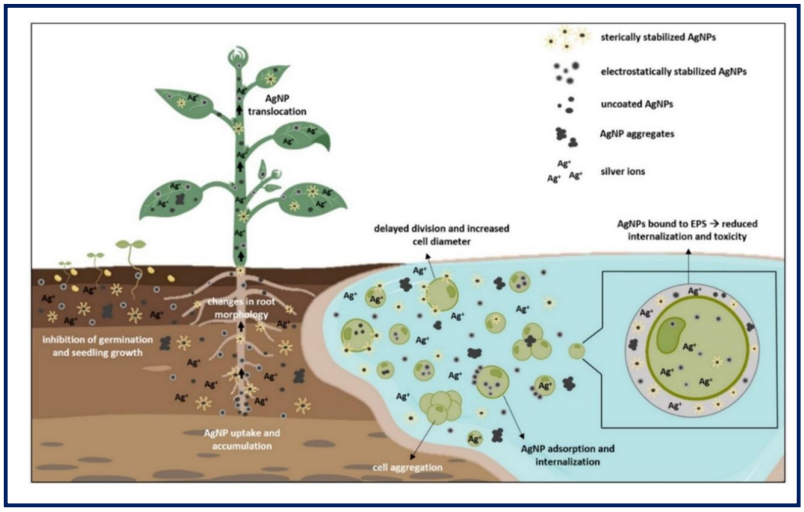

Fig. 10: Uptake of differently coated and uncoated AgNPs in plants and freshwater algae and their effects on growth and morphology. EPS extracellular polymeric substances. After Biba *et al.,* (2020)

Authors attributed this variance in results to the different size of seeds in question because smaller cabbage seeds with greater surface-to-volume ratio were found to be more prone to interaction with AgNPs Pokhrel *et al.,* (2013). Germination of tobacco seeds was also delayed and slower during the treatments with citrate-coated AgNPs, but effects on the seedling growth were shown to be concentration-dependent Biba *et al.,* (2021), Root growth was enhanced at lower tested concentrations but significantly reduced at higher concentrations. In tomato plants (*Lycopersicon esculentum*), citrate-coated AgNPs- had no effect on germination, but they significantly decreased root elongation, even in the lowest tested dose Song *et al.,* (2013). Adverse toxic effects of AgNP-citrate on growth of mung bean (*Phaseolus radiatus*) and great millet (*Sorghum bicolor*) were also reported Lee *et al.,* (2012). AgNPs caused necrosis and browning of the root tissue of both plant species that was consequently attributed to accumulated AgNPs in the cells, as confirmed by TEM and X-ray energy dispersion spectroscopy (EDS). Geisler-Lee *et al.,* (2014) obtained an interesting finding in the research where no initial effects on germination of *A. thaliana* were detected upon exposure to citrate-coated AgNPs; however, negative effects were confirmed and amplified over the next three generations. Effects of sterically stabilized AgNP-PVP on germination and plant early growth are also adverse. Scherer *et al.,* (2019) observed AgNP-PVP internalization in roots of *A. cepa* that led to reduction of germination index and root elongation. A study conducted on wheat seedlings showed that AgNP-PVP negatively impacted root length and fresh mass upon treatment, even though germination percentage and germination rate were not affected Vannini *et al.,* (2014). Furthermore, silver content was higher in roots compared to the leaves of treated seedlings. However, TEM images could not confirm AgNP entry to the cells and observed root tip browning was ascribed to AgNPs adsorbed to the root tissue Vannini *et al.,* (2014). Different trends were observed in rocket (*Eruca sativa*) seeds; germination of the seed was also not affected upon treatment with AgNP-PVP, but root growth was significantly stimulated Vannini *et al.,* (2013). Another study showed similar silver uptake for castor bean (*Ricinus communis*) seedlings exposed to AgNP-PVP and AgNO3. However, AgNP-PVP had no significant impact on castor bean seed germination and growth, while ionic silver significantly decreased those parameters Yasur and Rani (2013).

In contrast, in the research of Wang *et al.,* (2020) in which AgNP-PVP was localized in the cell wall and intercellular spaces of A. thaliana roots, it was found that AgNPs promoted root growth at low concentrations. However, higher concentrations had the opposite effect, suggesting a dose-dependent response. Another hydrophilic molecule used in AgNP stabilization is PVA, which showed detrimental impact on growth and morphology of *L. punctata* with distinct signs of chlorosis Lalau *et al.,* (2020). Similar effects were reported for *O. sativa*, where higher doses induced AgNP-PVA penetration through the cell wall. Moreover, restricted root growth, decrease in dry weight, and significant damage of the cell morphology were revealed Mirzajani *et al.,* (2013). GA is another commonly used steric AgNP stabilizer. Yin *et al.,* (2011) found that AgNP-GA inhibited growth of *L. multiflorum* seedlings and significantly changed their root morphology, mainly observed as a lack of root hairs and damaged epidermis and root cap. These results were ascribed to high silver content measured in both roots and shoots of the seedlings. Moreover, detrimental effects of AgNP-GA were not mitigated with the addition of cysteine and were far more pronounced than the effects of ionic silver applied at same concentrations Yin *et al.,* (2011). Only a couple of research groups compared differently coated AgNPs in the same experimental setup in an attempt to deduce the impact of a particular stabilizing agent Biba *et al.,* (2021). Treatment of AgNP-GA resulted in germination and early growth of eleven wetland plants, which was not observed upon AgNP-PVP exposure Yin *et al.,* (2012). These findings, however, cannot be assigned completely to the coating molecule, since applied AgNPs had different sizes (20 nm for AgNP-PVP and 6 nm for AgNP-GA). Pereira *et al.,* (2018) reported that AgNP-PVP and AgNP-citrate caused harmful effects on Lemna minor upon treatment, but their mechanisms differed; AgNP-PVP affected growth rate, while AgNP-citrate induced chlorosis. Comparison effects of uncoated nanomaterials of AgNPs, AgNP-PVP, and AgNP-citrate on two developmental stages of bryophyte Physcomitrella patens revealed higher growth inhibition of protonema and leafy gametophyte in AgNP-citrate treatment compared to AgNP-PVP Liang *et al.,* (2018) .Discrepancy in effects between two developmental stages was found among the treatments with uncoated and citrate-coated AgNPs, i.e., uncoated AgNPs had higher impact on protonemal stage, while AgNP-citrate affected gametophyte stage more, which correlated with a significantly higher Ag uptake in the gametophyte tissue, due to higher rates of AgNP-citrate dissolution in the used medium over time Liang *et al.,* (2018). In research

conducted on tobacco seedlings, uptake of silver was similar for PVP- and CTAB-coated AgNPs and $AgNO_3$ Biba *et al.,* (2020).

However, germination tests and measurements of root length and fresh and dry weight revealed significantly higher toxicity of AgNP-CTAB compared to AgNP-PVP and even ionic silver. Furthermore, harmful effects of AgNP-CTAB were not reduced with the addition of cysteine, and treatment with CTAB alone exhibited similar results. This finding suggests that phytotoxicity of CTAB-coated AgNPs originates from the coating itself. Similar discovery was reported in a study of AgNP-PVP and AgNP-DDAB effects on pea (*Pisum sativum*), where higher doses of AgNP-DDAB and treatment with DDAB itself significantly reduced seed germination and root length, which was not observed in AgNP-PVP treatment Cvjetko *et al.,* (2017). Presented results showed differential response of plants during their early development concerning coatings used in AgNP treatment. To better understand the mechanism of AgNP phytotoxicity, it is imperative to include more coating-dependent studies in the future. Algal accumulation of AgNPs is an important process of AgNP transport through the aquatic ecosystem Wang *et al.,* (2019). AgNPs can be adsorbed onto the algae surface and/or internalized in the cell due to the porous structure of the cell wall Behra *et al.,* (2013), Prazak *et al.,* (2020). At normal conditions, only particles smaller than 20 nm can enter the algal cell, but during cell division and stress induction, cell wall permeability increases, allowing entry of even bigger sized particles , causing detrimental effects on their growth and morphology Kalman *et al.,* (2015) Xia *et al.,* (2015) . Uncoated AgNPs, which are highly unstable in a liquid medium, triggered significant cell aggregation and reduction of *C. vulgaris* viability Oukarroum *et al.,* (2012), Hazeem *et al.,* (2019). The additions of different coatings changes AgNP characteristics and subsequently alter its uptake dynamics and overall effects. Citrate-coated AgNPs had no effect on growth of C. Vulgaris Qian *et al.,* (2016) but significantly inhibited growth of *Microcystis aeruginosa* Qian *et al.,* (2016), Xiang *et al.,* (2018), showing differential effect of AgNPs on prokaryotic and eukaryotic algae. Romero *et al.,* (2020). Qian *et al.,* (2016) reported increase in cell diameter and biomass in *C. vulgaris* upon exposure to AgNP-citrate that was attributed to their delayed division rate. Growth reduction was also observed in AgNP-citrate-treated *E. gracilis*, where further analysis showed that toxicity was not particle-specific but rather the combination of Ag^+ uptake and AgNP adsorption on the cell surface Yue *et al.,* (2017).

Upon exposure to PVP-coated AgNPs, growth of *C. reinhardtii* was not disturbed, even though AgNPs were found in the periplasmic sp ace and cytoplasm. Furthermore, comparative experiments with Ag^+ exposure excluded the possibility of secondary AgNP formation inside the cell, suggesting AgNP entry into algal cell via cellular internalization Wang *et al.,* (2016). On the contrary, IC50 values showed concentration dependent toxicity of AgNP-PVP in *R. subcapitata* (formerly known as *Pseudokirchneriella subcapitata*), which was significantly mitigated with the addition of humic substances that prevent AgNP dissolution Wang *et al.,* (2015). Dose-dependent growth reduction was also measured in *Scenedesmus sp*. treated with AgNP-PVA Pham (2019). A higher toxicity of AgNP-citrate compared to AgNP-PVP toward growth of *R. subcapitata* was ascribed to their different dissolution rates Pham (2019), Kennedy *et al.,* (2010), Angel *et al.,* (2013). In a comparative study by Kalman *et al.,* (2015), AgNP-PVP and AgNP-citrate showed similar uptake rates and growth reduction in *C. vulgaris*, whereas AgNP-PEG treatment resulted in lower toxicity, even though its uptake was significantly faster. This effect could be attributed due to the existence of extracellular polymeric substances (EPS), a protective layer on algae surface Zhou *et al.,* (2016). EPS can promote AgNP aggregation and complex Ag^+, limiting overall AgNP bioavailability Miao *et al.,* (2009), Ribeiro *et al.,* (2015). Moreover, EPS negative charge could be the reason for nonuniform algae response toward treatment with differently coated AgNPs Peulen and Wilkinson (2011). Zhou *et al.,* (2016). have examined the role of EPS in *Chlorella pyrenoidosa* treated with AgNP-PVP and AgNP-citrate. Compared to AgNP-citrate, AgNP-PVP had lower cell internalization rate but higher adsorption constant. Further analyses revealed that AgNP-PVP strongly bind to EPS and have milder effect on plasmolysis and membranolysis than AgNP-citrate, whose highly negative charge limited adsorption onto the cell surface. Removal of EPS led to significant increase of AgNP internalization in both AgNP treatments, showing an important role of EPS in AgNP bioaccumulation. Since EPS evidently play an important role in bio–nano interactions, effects of differently coated AgNPs on EPS should be further investigated.

4.2. Phytotoxicity at Physiological Level

Phytotoxicity of AgNPs to plants at the physiological level is predicted by reduction of chlorophyll and nutrient uptake, decline of transpiration rate, and alteration of hormone. AgNPs can disrupt the synthesis of chlorophyll in leaves and, thus, affect the photosynthetic system of the plants Tripathi *et al.,* (2017). Qian *et al.,* (2014) showed that AgNPs could accumulate in *Arabidopsis* leaves, further disrupt the thylakoid membrane structure, and decrease chlorophyll content, leading to the inhibition of plant growth Qian *et al.,* (2014). Nair and Chung reported that, after exposure to AgNPs for one week, total chlorophyll and carotenoids contents were significantly decreased in rice (*Oryza sativa L.*) seedlings Nair and Chung (2014). Vishwakarma *et al.,* (2017) found that AgNPs could accumulate in mustard (*Brassica sp.*) seedlings and caused severe inhibition in photosynthesis Vishwakarma *et al.,* (2017). A recent study showed that AgNP exposure changed the thylakoid in Physcomitrella patens, and AgNPs decreased the chlorophyll b content and disturbed the balance of some essential elements in the leafy gametophytes Liang *et al.,* (2018) Fig. (11).

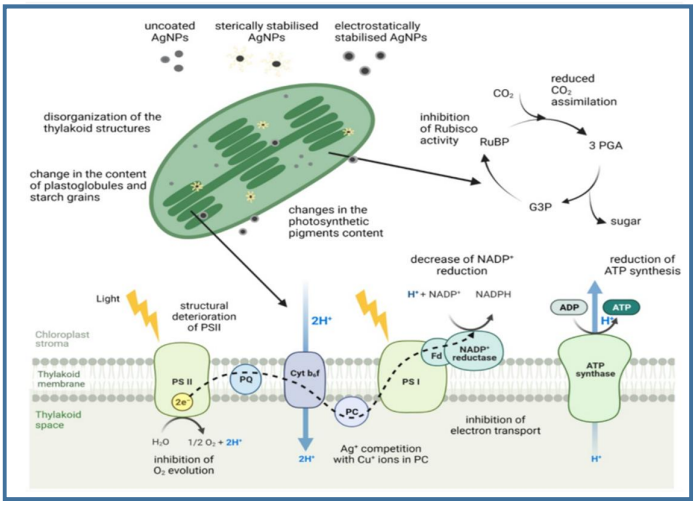

Fig. 11: Structural and functional changes of the photosynthetic apparatus in plants and freshwater algae upon exposure to AgNPs with different surface coatings. RuBP—ribulose 1,5-bisphosphate, 3-PGA—3-phosphoglyceric acid, G3P—glyceraldehyde 3-phosphate, PS—photosystem, PQ— plastoquinone, Cyt b6f—cytochrome b6f, PC—plastocyanin, Fd—ferredoxins. Figure was adapted from "Light Dependent Reactions of Photosynthesis After Biorender (2021).

Exposure of *Lupinus termis L.* seedlings by AgNPs, particularly after ten days, significantly reduced the shoot and root elongation and fresh weights, total chlorophyll, and total protein contents Al-Huqail *et al.,* (2018) Fig. (12).

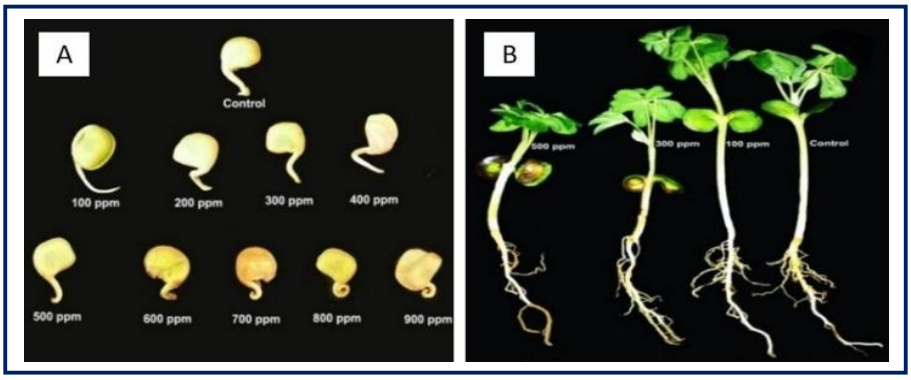

Fig. 12: Illustrates, (A) Effect of different concentrations of CSL-AgNPs (0–900 ppm) on Lupinus termis L seed germination. (B) Effect of different concentrations of CSL-AgNPs (0, 100, 300 and 500 ppm) on growth parameters of Lupinus termis L. After Al-Huqail *et al.,* (2018)

In *Cucurbita pepo*, the rate of transpiration was remarkably reduced after AgNP exposure Stampoulis *et al.,* (2009), Hawthorne *et al.,* (2012), Musante and White (2012). In addition, AgNPs can affect the fluidity and permeability of the membrane and, consequently, influence water and nutrient uptake. Zuverza-Mena *et al.,* (2016) demonstrated that AgNP exposure on radish (*Raphanus sativus*) sprout caused a decrease in water content in a dose-dependent manner; the nutrient content (Ca, Mg, B, Cu, Mn, and Zn) was also significantly reduced, suggesting that AgNPs may affect plant growth by changing water and nutrient . It was reported that AgNPs also affect plant hormones Fig (13).

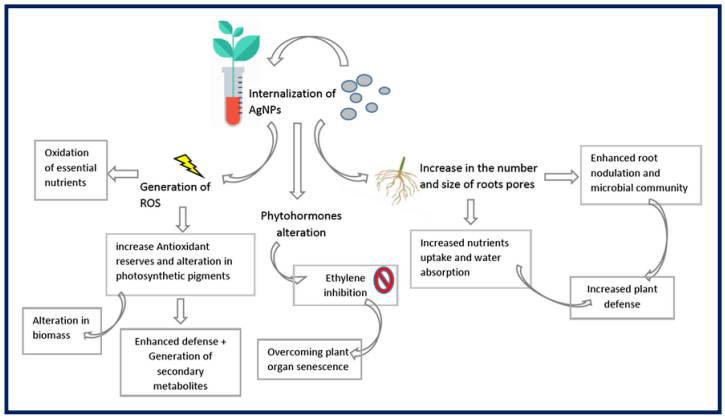

Fig. 13: Overview of mechanism of action of AgNPs on plants

Sun *et al.,* (2017) reported that the root gravitropism of *Arabidopsis* seedling was inhibited by exposure to AgNPs in a dose-dependent manner. Further analysis indicated that AgNPs reduced auxin accumulation, while gene expression analysis suggested that auxin receptor-related genes were down regulated upon AgNP exposure. Vinkovi´c *et al.,* (2017) conducted hormonal analysis using ultra-high-performance liquid chromatography electrospray, and found that AgNP accumulation in pepper tissue resulted in a significant increase in total cytokinin levels, suggesting the importance of cytokinin in the plant's response to AgNPs stress. Wang *et al.,* (2017) found that Ag2S-NPs could reduce the growth of cucumber and wheat; expressions of six genes involved in ethylene signaling pathway were significantly up regulated in cucumber after exposure to Ag2S-NPs, suggesting that Ag2S-NPs could affect plant growth through an interface with the ethylene-signaling pathway

4.3. Cytotoxicity and Genotoxicity

AgNPs can also cause toxicity at the cellular and molecular level in plants. Many studies showed that the inhibition of plant growth after AgNP exposure is accompanied with alteration of cell structure and cell division Fig. (14).

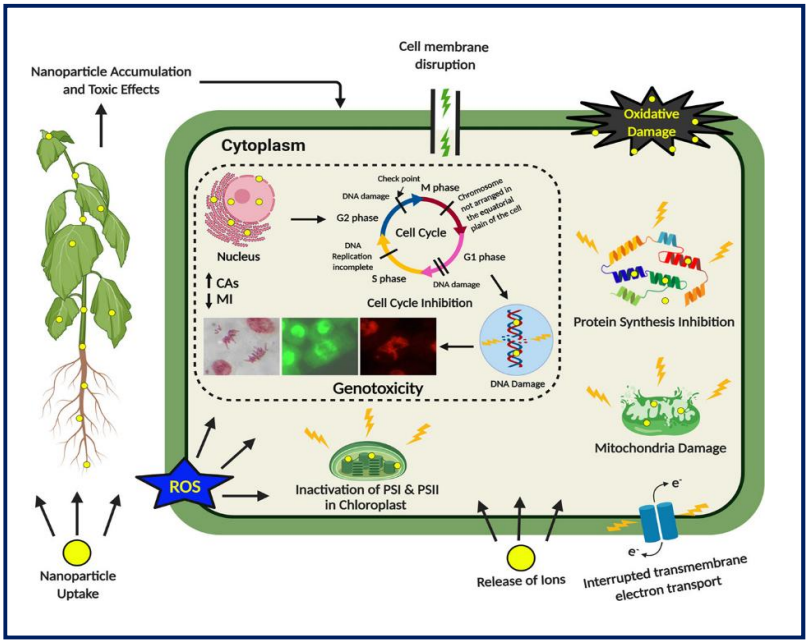

Fig. 14: Illustrates the uptake, translocation, and bioaccumulation of NMs in plants, focusing on their inhibitory effects and mechanisms involved within plants. After Murali *et al.,* (2022)

Murali *et al.,* (2022), the current advancement in nano-metallic caused phytotoxicity on living organisms and current challenges in crops. Provide new tools in agriculture to boost sustainable, but the main concern is that large-scale production and release of nanomaterials (NMs) into the ecosystem is a rising threat to the surrounding environment that is an urgent challenge to be addressed. The usage of NMs directly influences the transport pathways within plants, which directly relates to their stimulatory inhibitory effects. Because of the unregulated (NMs) exposure to soil, they are adsorbed at the root surface, followed by uptake and inter/intracellular mobility within the plant tissue, while the aerial exposure is taken up by foliage, mostly through cuticles, hydathodes, stigma, stomata, and trichomes, but the actual mode of NMs absorption into plants is still unclear. NMs-plant interactions may have stimulatory or inhibitory effects throughout their life cycle depending on their composition, size, concentration, and. Although many publications on NMs interactions with plants have been reported, the knowledge on their uptake, translocation, and bioaccumulation is still a question to be addressed by the scientific community. One of the critical aspects that must be discovered and understood is detecting NMs in soil and the uptake mechanism in plants. Therefore, the nanopollution in plants has yet to be completely understood regarding its impact on plant health, making it yet another artificial environmental influence of unknown long-term consequences

Yin *et al.,* (2011) found that Lolium multiflorum seedlings failed to develop root hair, and the cortical cells were highly vacuolated and collapsed, while the epidermis and root cap were also damaged after exposure to 40 mg/L AgNPs. Pokhrel and Dubey (2013) reported that Ag NPs could reduce the size of the vacuole and lead to the reduction of cell turgidity and cell size in maize (*Zea mays L.*) and cabbage (*Brassica oleracea var. capitata L.*) Tripathi et al,. (2017).Similarly, Mazumdar found that after AgNPs enter the cell of Brassica campestris; vacuoles and cell wall integrity were damaged, and other organelles might also be affected Abdelsalam *et al.,* (2018) , Mazumdar (2014) . Likewise, Mirzajani etal (2013) found that AgNPs with a concentration of to 60 µg/mL could penetrate the cell wall, and damage the cell morphology and its structure in rice. In addition, Kumari and Mukherjee (2009) reported that AgNP exposure in Allium cepa significantly decreased the mitotic index and impaired cell division, resulting in Chromatin Bridge, stickiness, disturbed metaphase, multiple chromosomal breaks, and cell disintegration. Similarly, Patlolla etal (2012) demonstrated that AgNP treatment significantly increased the chromosomal aberrations and micronuclei, and decreased the mitotic index (MI) in root tip cells of broad bean (*Vicia faba L.*), suggesting that cell cycle and mitosis in root tip cells was disrupted by AgNPs . A recent study confirmed that the root tip cells of wheat could

readily internalize the AgNPs. After AgNP internalization, the root tip cells exhibited various types of chromosomal aberrations, such as incorrect orientation at metaphase, chromosomal breakage, spindle dysfunction, fragmentation, unequal separation, and distributed and lagging chromosomes, which seriously interfered with cell function Abdelsalam *et al.,* (2018) . The uptake, translocation, and major phytotoxicity of AgNPs in plants Fig. (15).

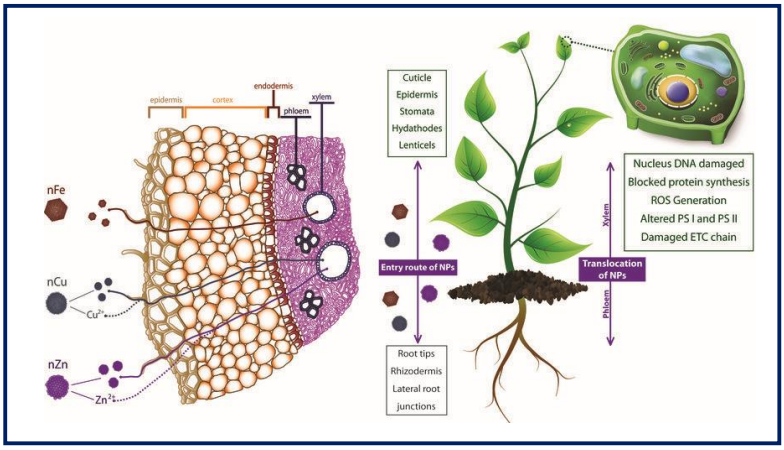

Fig. 15: Schematic presentations of nanoparticles uptake, translocation and phytotoxicity After Rajput *et al.,* (2019).

5. Toxicity Mechanisms

5.1. AgNP-Induced Oxidative Stress

The phytotoxicity mechanism of AgNPs, resulting in oxidative stress in plant cells Tripathi *et al.,* (2017), Nair *et al.,* (2010), induce the production of excess reactive oxygen species (ROS). A number of studies demonstrated that ROS production is significantly elevated in plants after exposure to AgNPs. There are four types of ROS produced in plant cells, including singlet oxygen (1^{O2}), superoxide ($O2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($HO^{\bullet}$) Ma *et al.,* (2015), Mourato *et al.,* (2012) Studies published suggesting that exposure to metal NPs can induce increased generation of reactive oxygen species (ROS) Yang etal (2017) , which can react with proteins, lipids and DNA molecules, resulting in a number of metabolic disorders, destruction of cell membranes and, in consequence, cell death. Production of superoxide radicals O^{-2} and hydrogen peroxide (H_2O_2), common ROS, was studied by Panda *et al.,* (2011), who reported their increased levels in A. cepa roots after 2h-exposure to AgNPs (37nm, 0, 5, 10, 20, 40, 80mg L^{-1}) Fig.(16).

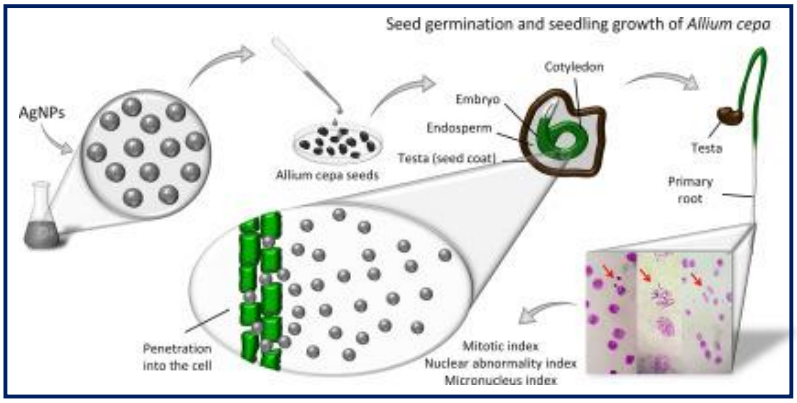

Fig. 16: Illustrates Cytotoxic and genotoxic effects of silver nanoparticles on meristematic cells of *Allium cepa* roots. After Scherer *et al.,* (2019)

Exposure of rice seedlings to 0.5 and 1mg L^{-1} of 20nm AgNPs also resulted in a dose-dependent increase of O^{-2} and H_2O_2 in roots and shoots after 1 week Nair and Chung (2014). Studies of Galazzi *et al.,* (2019) elevated H_2O_2 production in transgenic soybean (Glycine max) plants was found after 14-days-treatment with 50 mgkg $^{-1}$ of 60 nm AgNP-citrate, while increase in ROS production was also observed in rice seedlings exposed to uncoated AgNPs (18.34nm and concentration 30 and 60µgm L^{-1}) for 7, 14 and 21 days Mirzajani *et al.,* (2013). A significant dose-dependent increase of ROS was also found after exposure of aquatic plants Lemna gibba to 1 and 10mg L^{-1} of 50nm AgNPs Nair and Chung (2014) and S. polyrhiza to 0.5, 1.0, 5.0 and 10mg L^{-1} of 6nm AgNPs Jiang etal (2014). In the study of Cvjetko *et al.,* (2018), exposure of A. cepa roots to AgNPs stabilized with three different surface coatings, citrate (AgNP-citrate; 61.2 nm), polyvinylpyrrolidone (AgNP-PVP; 9.4nm) and cetyltrimethyl ammonium bromide (AgNP-CTAB; 5.6 nm), resulted with significant increase in ROS content compared to the control at concentrations of 50, 75 and 100 µM, with AgNP-PVP and AgNP-CTAB exhibiting concentration-dependent increase. Moreover, in the same study AgNP-treatments exhibited lower toxicity compared to exposure with $AgNO_3$ indicating AgNP toxicity is not necessarily associated with dissociation of Ag^+ ions.

Scherer *et al.,* (2019) stated that harmful effects of silver nanoparticles (AgNPs) have been confirmed in many organisms, but the mechanism of their toxicity is not yet fully understood. In biological systems, AgNPs tend to aggregate and dissolve, so coatings that influence their physicochemical properties often stabilize them. The effects of AgNPs with different coatings [polyvinylpyrrolidone (PVP) and cetyltrimethylammonium bromide (CTAB)] on oxidative stress appearance and proteome changes in tobacco (*Nicotiana tabacum*) seedlings have been examined. To discriminate between the Nanoparticulate Ag forms from the ionic one, the treatments with $AgNO_3$, a source of Ag^+ ions, were also included. Ag uptake and accumulation were found to be similarly effective upon exposure to all treatment types, although positively charged AgNP-CTAB showed less stability and a generally stronger impact on the investigated parameters in comparison with more stable and negatively charged AgNP-PVP and ionic silver ($AgNO_3$). Both AgNP treatments induced reactive oxygen species (ROS) formation and increased the expression of proteins involved in antioxidant defense, confirming oxidative stress as an important mechanism of AgNP phytotoxicity. However, the mechanism of seedling responses differed depending on the type of AgNP used. The highest AgNP-CTAB concentration and CTAB coating resulted in increased H_2O_2 content and significant damage to lipids, proteins and DNA molecules, as well as a strong activation of antioxidant enzymes, especially CAT and APX. On the other hand, AgNP-PVP and $AgNO_3$ treatments induced the nonenzymatic antioxidants by significantly increasing the proline and GSH content. Exposure to AgNP-CTAB also resulted in more noticeable changes in the expression of proteins belonging to the defense and stress response, carbohydrate and energy metabolism and storage protein categories in comparison to AgNP-PVP and $AgNO_3$. Cysteine addition significantly reduced the effects of AgNP-PVP and $AgNO_3$ for the majority of investigated parameters, indicating that AgNP-PVP toxicity mostly derives from released Ag^+ ions. AgNP-CTAB effects, however, were not alleviated by cysteine addition, suggesting that their toxicity derives from the intrinsic properties of the nanoparticles and the coating itself.

Under normal environmental conditions, ROS are generated as byproducts of normal metabolic pathways in organelles such as chloroplasts, mitochondrion, and peroxisomes Ma *et al.,* (2015), Møller *et al.,* (2007). Under stressed conditions, however, excessive amounts of ROS are generated and cause severe oxidative damage to plant biomolecules through electron transfer Carocho *et al.,* (2013). The production of excess ROS induced by AgNP exposure can subsequently lead to oxidative stress, cause peroxidation of polyunsaturated fatty acids (known as lipid peroxidation), and damage the cell membrane permeability. Cell structure, directly damaging protein and DNA, resulting in potential cell death and growth inhibition in plants Ma *et al.,* (2015), Tripathi *et al.,* (2017),, Capaldi Arruda *et al.,* (2015), Yuan *et al.,* (2018).

Panda *et al.,* (2011) stated that AgNP-P (phyto-synthesized from silver nitrate $AgNO_3$) or AgNP-S (commercial AgNPs from Sigma–Aldrich) application in Allium cepa significantly increased the generation of superoxide ($O2^{\bullet-}$) and H_2O_2 they also induced cell death to different extents in a dose-dependent fashion, following an order of AgNP-S > AgNP-P at doses ≥20 mg/L. Moreover, AgNP-P significantly decreased the mitotic index. Comet assay suggested that DNA damage was significantly enhanced after AgNP-P and AgNP-S treatments in a dose-dependent manner, whereby AgNP-S (threshold dose ≥ 10 mg/L) is more genotoxic than AgNP-P (threshold dose ≥ 20 mg/L). Qian etal

(2013) found that AgNPs could accumulate in Arabidopsis leaves and change the transcription of antioxidant and aquaporin genes, suggesting that AgNPs can change the balance between oxidant and antioxidant systems. Similarly, Speranza *et al.,* checked the in vitro toxicity of AgNPs to kiwifruit pollen, and found that changes in ROS generation paralleled the entire germination dynamics of kiwifruit pollen. The AgNP treatment delayed H_2O_2 production, whereas AgNPs dramatically induced ROS overproduction at the late stage during pollen germination, leading to decreases in pollen viability and performance Speranza *et al.,* (2013). Moreover, De La Torre-Roche *et al.,* (2013) found that AgNP exposure with concentration at 500 and 2000 mg/L caused significant increases Stampoulis *et al.,* (2009), 75%) in malondialdehyde (MDA) formation in soybean (Glycine max) MDA is a major peroxidation product under stress conditions and is indicative of the extent of lipid peroxidation Lin *et al.,* (1996). Nair and Chung (2014) reported that lipid peroxidation increased significantly after exposure to 0.2, 0.5, and 1 mg/L AgNPs. In Arabidopsis in rice, exposure to 0.5 and 1 mg/L AgNPs resulted in a significant increase in H_2O_2 formation and lipid peroxidation in shoots and roots; further analysis suggested that AgNPs promoted ROS production in a dose-dependent manner. Thiruvengadam *et al.,* (2015) reported the impact of AgNP exposure in turnip seedlings, and found that a higher concentration of AgNPs caused excessive generation of superoxide radicals and increased lipid peroxidation; H_2O_2 formation was also significantly increased after exposure to 5 and 10 mg/L AgNPs. Dichlorofluorescein (DCF) fluorescence indicated a sharp increase in ROS production in turnip seedling roots, suggesting the existence of oxidative stress in the roots after AgNP exposure. Further analysis by comet assay and terminal deoxynucleotidyl transferase-mediated dUTP nick end labeling (TUNEL) assay confirmed that DNA damage was significant, suggesting that AgNPs can induce cell death through apoptosis.

This result can attributed to AgNPs coatings, since addition of coating can stabilize nanoparticles, reducing dissociation of Ag^+ ions and thus diminish its toxicity Yasur and Rani (2013). Nair and Chung (2014) reported high concentration-dependent increase of ROS formation in $AgNO_3$-treated Arabidopsis seedlings compared to AgNP-treated ones. Moreover, in the study of tobacco seedlings exposed to citrate-coated AgNPs for 30 days it was found that higher concentrations of 50 nm AgNPs (100µM) induced elevated production of ROS. However, despite the higher accumulation of Ag in seedlings exposed to AgNPs than in those treated with $AgNO_3$, effects of $AgNO_3$ were to be more toxic than those of nanoparticles Peharec *et al.,* (2018) Fig. (17).

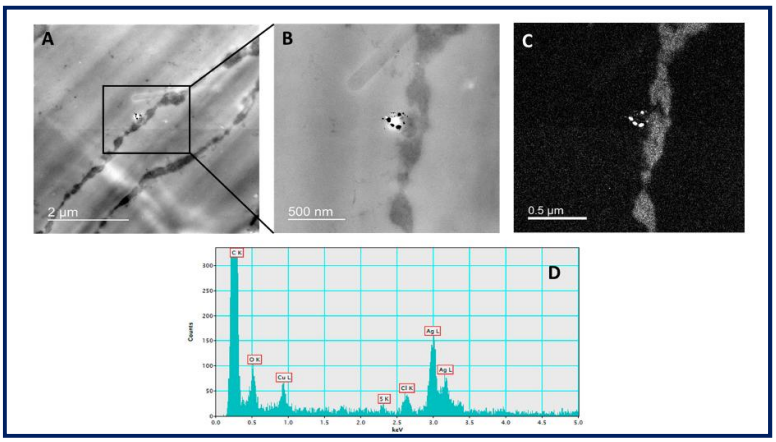

Fig. 17: Localization of AgNPs in the root cells of tobacco seedlings treated with 100 µM AgNP-PVP. TEM microphotographs of root cell with AgNPs in the vacuole of the epidermal cell (A), enlarged part of epidermal cell with AgNPs (B), silver elemental map and (C) energy-dispersive X-ray spectrum (D).After Biba *et al.,* (2022)

On the contrary, higher accumulation of total ROS and O_2 in potato (*Solanum tuberosum*) plantlets exposed to 20 nm uncoated AgNPs was recorded in comparison to $AgNO_3$-exposed ones after application of 10 and 20mg L^{-1} concentrations of both silver forms Homaee and Ehsanpour (2016). Suggesting the effects of AgNPs on ROS production are not unambiguous. The study in which adult

tobacco plants were treated with 61nm AgNP-citrate (25, 50, 75, 100 and 500 µM) no changes in ROS accumulation were recorded in comparison to the control Peharec *et al.,* (2018) thus, suggesting that the response to AgNP-imposed stress might also be dependent on the plant developmental stage. Still, in the majority of presented studies, AgNPs of different sizes, concentrations and coatings induced ROS formation, regardless of the duration of the exposure and investigated plant species. Therefore, toxicity of AgNPs in plant cells in majority of the cases can be attributed to the generation of ROS, whose production might explain the effects of nanoparticles on plants. However, at this point it cannot be stated with certainty if AgNPs induce generation of ROS directly or indirectly through Ag^{+} ions. When generation of ROS exceeds the capacity of the cellular antioxidant defence system, oxidative stress occurs, which may lead to inactivation and damage of membrane lipids, proteins and DNA molecule. Malon di-aldehyde (MDA) is one of the final products of oxidative modification of lipids, and changes of its concentration indicate membrane lipid peroxidation under ROS action as the effect of cellular injury of membrane lipids. It is widely used as an indicator of oxidative stress in plant cells and tissues McDaniel and Binder (2012). Beside lipid peroxidation, protein oxidation, one of the covalent modifications of proteins induced by ROS or other products of oxidative stress, is also often analyses to confirm the presence of oxidative stress. Increased level of lipid peroxidation was reported for rice Nair and Chung (2014), *Arabidopsis* Nair and Chung (2014) and mung bean Nair and Chung (2015) seedlings exposed to AgNPs. In the study of Cvjetko *et al.,* (2018), in which effects of AgNPs stabilized with different coatings were analyzed, it was found that treatments of *A. cepa* roots with 5.6nm AgNP-CTAB exhibited concentration-dependent increase in MDA and carbonyl content, while exposure to 60nm AgNP-citrate and 9.4nm AgNP-PVP resulted with significantly lower values, which was partially attributed to the smaller size of AgNP-CTAB. The very small size of NPs is believed to cause higher toxicity in plants and uptake of AgNPs has been already associated with particle size and concentration Silva *et al.,* (2014).

Moreover, the strong effect of CTAB-coated AgNPs can also be attributed to the coating itself because the cell membrane is negatively charged and may enter into electrostatic interactions with the AgNP-CTAB, due to positively charged CTAB. The weakest impacts were recorded for citrate-coated AgNPs, which were of the biggest size; namely, due to the formation of the aggregates as well as to negative charge, the uptake of AgNP-citrate by *A. cepa* root cells was probably somewhat difficult and the AgNPs surface available for interaction with organic molecules decreased inko *et al.,* (2014) thus, lowering their toxic effects. In the study of Barbasz *et al.,* (2016), two wheat callus cultures, one sensitive to oxidative stress and the tolerant one, were exposed to 20, 40 and 60 ppm of 17nmAgNPs and it was found that a stronger increase of MDA content was observed in sensitive cultivar than in the cells of tolerant callus. Peharec *et al.,* (2018) reported that in tobacco seedlings increased contents of MDA and protein carbonyls were recorded only after the highest concentration (100µM) of the 50nm AgNP-citrate was applied. However, after exposure of adult tobacco plants to the same concentrations of AgNP-citrate, none of the applied AgNP-concentrations neither induced a significant increase in MDA and protein carbonyl content in roots nor in leaves Cvjetko *et al.,* (2018) thus, suggesting that plant response to AgNPs might be also dependent on plant age and/or developmental stage.

In several studies, comparison between plants exposed to AgNPs with those exposed to the same concentration of $AgNO_3$ was performed Fig. (18).

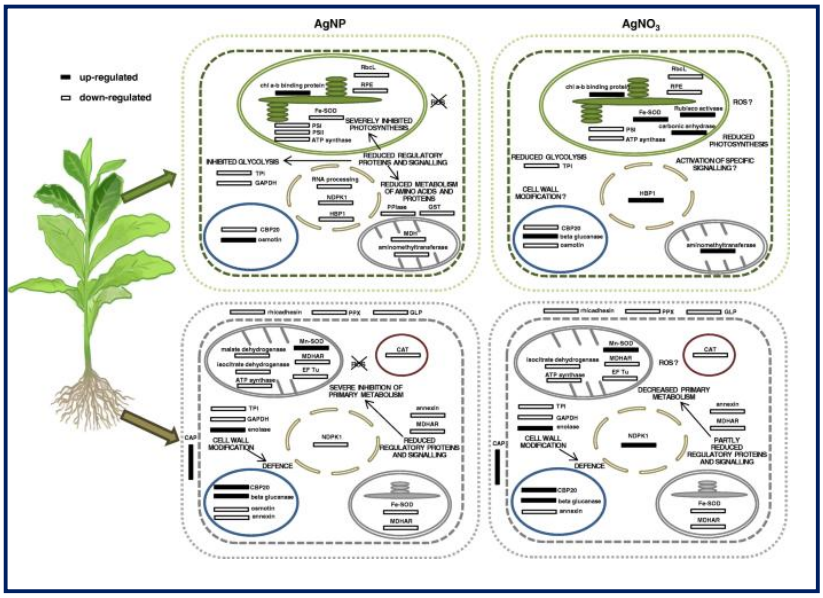

Fig. 18: A schematic comparison of protein abundance in roots and leaves of tobacco adult plant in response to exposure to 100 µM AgNPs or 100 µM AgNO3. CAP, cysteine-rich secretory protein; CAT, catalase; CBP 20, cap-binding protein 20; EF Tu, elongation factor Tu; Fe-SOD, iron-dependent superoxide dismutase; GAPDH, glyceraldehyde-3- phosphate dehydrogenase; GLP, germin-like protein; GST, glutathione S-transferase; HBP1, ankyrin-repeat protein HBP1; MDH, malate dehydrogenase; MDHAR, monodehydroascorbate reductase; Mn-SOD, manganese-dependent superoxide dismutase; NDPK1, nucleoside diphosphate kinase 1; PPIase, peptidyl-prolyl cis-trans isomerase; PPX, peroxidase; PSI, photosystem I proteins; PSII, photosystem II proteins; RbcL, Rubisco large subunit; RPE, ribulose-phosphate 3-epimerase; Rubisco activase, ribulose-1,5-bisphosphate carboxylase/oxygenase activase; TPI, triose phosphate isomerase. After Peharec *et al.,* (2019)

Peharec *et al.,* (2019) stated that high overlap of differently abundant proteins between AgNP and $AgNO_3$ treatments was found in tobacco roots, but in leaf tissue, almost a half of the proteins exhibited different abundance level between AgNP exposure and $AgNO_3$ exposure. A schematic comparison of protein abundance in the roots and leaves of tobacco adult plant in response to exposure to 100 µM AgNPs or 100 µM $AgNO_3$ has been generated Fig. (18). Obtained results indicated that AgNPs and $AgNO_3$ caused similar changes in the root proteome, but more distinct changes in the proteome of the leaf cells, although in both tissues, AgNPs induced higher suppression of protein abundance. Several proteins in roots, such as osmotin, NDPK1, and GS, were decreased only by AgNP treatment. These data confirm evidences found in other organisms Domingos *et al.,* (2011) Poynton *et al.,* (2012) that AgNP effects on the gene expression patterns are not only due to the dissociated Ag^+ ions. Interestingly, only several proteins (osmotin, basic beta-1,3-glucanase, CBP20, Fe-SOD, glyceraldehyde-3-phosphate dehydrogenase (GAPDH), triose phosphate isomerase (TPI), and MDH) were found to be regulated by silver treatments in both tobacco tissues. This tissue dependent response probably results from differences in metal content, as silver accumulation in roots was several times higher than in leaves, after both types of treatments Lee *et al.,* (2010).

$AgNO_3$-exposure imposed greater stress than AgNP-exposure Cvjetko *et al.,* (2018) , Peharec *et al.,* (2018) , Barbasz *et al.,* (2016) , which confirms that Ag^+ is generally more toxic for plants than Ag nanoparticles and that the AgNP-toxicity probably does not depend solely on the Ag^+ ions dissociated from nanoparticles. However, in some cases the results are not unambiguous. For example, Galazzi *et al.,* (2019) reported that after exposure of non-transformed (NT) and transformed (T; which after transformation gained tolerance to herbicide) soybean plants to AgNPs and $AgNO_3$ for 14 days, increase in MDA content was recorded for both soybean genotypes. However, in NT plants increase was much higher after exposure to $AgNO_3$ compared to AgNPs, while in T plants MDA content was of similarly elevated values after both types of treatments. This suggests that various factors might influence plant's

response to AgNP-imposed stress. Considering the impact on the DNA molecule, AgNPs were found to induce DNA damage Cvjetko *et al.,* (2018), Peharec *et al.,* (2018) and influence gene expression Patlolla *et al.,* (2012), Qian *et al.,* (2013), Saha and Gupta (2017). Kumari *et al.,* (2009) reported that uncoated AgNPs (100nm, 25, 20, 75, and 100ppm) may have a genotoxic effect in *A. cepa* roots, while in the same plant species it was found that biologically synthesized AgNPs of 20nm applied in 5, 10 and 20µgm L^{-1} concentrations caused severe mitotic and meiotic abnormalities in the root tips and flower bud cells Saha and Gupta (2017). Moreover, Patlolla *et al.,* (2012) demonstrated that 25, 50 and 100mg L^{-1} concentrations of 60nm uncoated AgNPs significantly increased the number of chromosomal aberrations, micronuclei, and decreased the mitotic index in exposed *V. faba* roots compared to control. Decrease in mitotic index was also found after exposure of *A. cepa* roots to 100µM AgNP-PVP and AgNP-CTAB Cvjetko *et al.,* (2018).

The overall results indicated that ROS formation and oxidative stress can play a critical role in phytotoxicity mechanism but AgNP size, overall surface charge and/or surface coating as well as on the plant species and developmental stage may influence plant response to AgNPs. Plants have developed very efficient ROS scavenging system, which depends on the activity of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR) and stimulate the production of antioxidant molecules such as ascorbic acid (AsA) and glutathione (GSH). Most of the studies dealing with AgNPs impact on plants reported changes in activities of antioxidant enzymes, although results are not unambiguous. Within a cell, the SOD constitutes the first line of defence against ROS since its neutralization of superoxide radical to H_2O_2 is very effective in preventing damage to biologically important molecules. Vannini *et al.,* (2014) reported increased SOD activity and expression after exposure of rocket seedlings to treatments with 10mg L^{-1} of 10nm AgNP-PVP. Peharec *et al.,* (2018) found enhanced SOD activity in tobacco seedlings exposed to AgNPs, which was in agreement with the low level of oxidative damage found in that tissue.

The induction of SOD activity was additionally confirmed in the same study by proteomic analysis, where up-regulation of Fe-SOD was found. Significant increase in SOD activity was also reported for potato plantlets exposed to AgNPs Homaee and Ehsanpour (2016). In callus cultures of two wheat varieties, treatments with AgNPs did not cause a significant change in SODs activity in the variety tolerant to oxidative stress, suggesting that in the tolerant callus, other antioxidants, such as GSH, whose increased content was measured, may be involved in cell protection, and/or, applied nanoparticle concentrations were not stressful for this variety Barbasz *et al.,* (2016). On the other hand, in the sensitive wheat callus, changes in SOD activity were concentration-dependent, thus indicating a mobilization of enzymatic antioxidant systems.

A slight decrease in SOD activity was observed in non-transformed soybean plants after treatment with AgNPs, while exposure of transformed, herbicide tolerant plants resulted with much higher increase in activity of this enzyme Galazzi *et al.,* (2019),. However, a strong increase in the CAT activity was detected in both soybean genotypes AgNPs, which suggests that this antioxidant enzyme has a key role in the protection against the toxic effects of ROS generated by AgNPs. These findings suggest that AgNPs phytotoxicity might be dependent on the sensitivity of the particular plant species or even on the cultivar or a variety of the same species. To protect cells against ROS completely, antioxidant enzymes such as CAT, PPX and APX have to remove H_2O_2 generated by SOD dismutation of O_2. Moreover, GR and GSH are two major components of AsAGSH pathway, which also plays a significant role in protecting cells against ROS. Significant increase in the activities of CAT, APX and GR was found after exposure of potato plantlets to AgNPs, and $AgNO_3$ Barbasz *et al.,* (2016).; however, in AgNP-treated plantlets, GR activity was significantly decreased at higher concentration, which was accompanied with higher reduction in GSH and AsA compared to plants exposed to $AgNO_3$, according to which authors suggested that AgNPs had higher toxicity than the equivalent mass of Ag ions. Homaee and Ehsanpour (2016) reported an increase of GSH levels in callus cells of both wheat genotypes exposed to AgNPs at all used concentrations (20, 40 and 60ppm); however, the greater change of GSH content was recorded in the tolerant variety in comparison to the sensitive one, which indicated that this nonenzymatic compound was the main antioxidant, the synthesis of which was activated in the tolerant variety in conditions of oxidative stress induced by AgNPs.

In the sensitive variety, a smaller increase in GSH level was accompanied with simultaneous activation of SOD and PPX; therefore, authors suggested that in the defense mechanism against AgNP-imposed stress, both enzymatic and nonenzymatic antioxidants are operating Barbasz *et al.,* (2016). In

the study performed on *A. cepa* roots, AgNP treatments induced the PPX activity, while significant concentration dependent decrease in CAT and APX activities was noticed, suggesting that PPX was the enzyme involved in lowering the ROS level Cvjetko *et al.,* (2017). Elevation of PPX and inhibition of CAT activity has also been reported in B. monnieri Krishnaraj *et al.,* (2012) and sensitive wheat calli Barbasz *et al.,* (2016) after exposure to AgNPs. The highest reduction of CAT activity observed in both sensitive and tolerant wheat calli at the highest applied concentrations of AgNPs corresponded with the highest amount of generated ROS, which indicates that CAT synthesis was probably inhibited by strong oxidative stress Barbasz *et al.,* (2016).

After exposure of castor bean seedlings to AgNPs, increase in PPX activity was not concentration-dependent, while CAT activity was inhibited Yasur and Rani (2013). In the study of Peharec *et al.,* (2018), elevated APX activity, along with the decreased PPX and unchanged CAT activity, suggested that APX was a key enzyme responsible for catalyzing the conversion of H_2O_2 into H_2O after exposure of tobacco seedlings to AgNPs. On the other hand, increased CAT activity was recorded in *S. polyrhiza* Jiang *et al.,* (2014) and water hyacinth (*Eichhornia crassipes*) Rani *et al.,* (2016) exposed to AgNPs. In roots of adult tobacco plants, exposure to AgNPs did not induce significant changes in activity of PPX, while lower AgNPs concentrations induced higher CAT activity, which was is in good correlation with no measurable changes in oxidative stress parameters, indicating that AgNPs induced mild oxidative stress, which could be efficiently alleviated by antioxidant enzymes Cvjetko *et al.,* (2018). The same study showed that in leaf tissue, no changes were recorded in APX activity, while PPX activity increased at lower concentrations and decreased at higher concentration Cvjetko *et al.,* (2018).

Moreover, AgNPs did not induce any significant oxidative stress in tobacco leaves. Since the Ag concentration in leaves was much lower than in roots, it is possible that some of the changes observed in the leaves were just a consequence of the stressful events that took place in the roots. A decrease in PPX activity at higher AgNP concentrations, after an initial increase at lower concentrations, was also recorded in leaves of *Pelargonium zonale* plants Hatami and Ghorbanpour (2013). Several reports in which AgNP toxicity was compared with those of $AgNO_3$ Cvjetko *et al.,* (2018), Peharec *et al.,* (2018) suggested that exposure to $AgNO_3$ induced severe oxidative stress accompanied with stronger response of antioxidant enzymes; in some cases even severe inhibition of activity was observed Yasur and Rani (2013) , possible due to Ag^+ binding to SH groups in enzymes. However, similar effects between AgNP- and $AgNO_3$-exposure were also observed Barbasz *et al.,* (2016). Moreover, it has been demonstrated that AgNPs were even more toxic than Ag^+ Qian *et al.,* (2013) and could alter the transcription of genes involved in antioxidant synthesis and change the balance between the oxidant and antioxidant systems. Presented results suggest that different antioxidant enzymes could play key roles in eliminating ROS accumulated because of nanosilver exposure but the exact mechanism of AgNP action on antioxidant system in plants is yet to be proven. Results obtained on oxidative damage to lipids, proteins, and DNA molecule as well as on changes in the activity of plant antioxidant enzymes in plants treated with AgNPs suggested that oxidative stress could have an important role in the phytotoxicity of AgNPs**.**

6. Physiological effect of AgNPs on plants.

6.1. Seed germination and plant growth

Impact of AgNPs on plant development was investigated in many studies through seed germination. The germination rate and root length are measured through growth of seedlings and plants, root/shoot elongation and dry weight are used to assess acute effects of NP form of silver on plant physiology. Tripathi *et al.,* (2017) stated that biosynthesized of AgNPs at 22 nm in different concentration (1000, 3000 and 5000µM in Hoagland medium) gradually significantly decreased pea (*Pisum sativum*) seed germination Fig. (19). similarly by Barrena *et al.,* (2009), they observed that application of 100 µg mL^{-1} of laboratory-synthesized AgNPs (29 nm) significantly reduced the germination index of cucumber and lettuce. El-Temsah and Joner (2012) reported that three types of AgNPs with different particle sizes (2 , 5 and 20 nm), applied in 0–100 mg $mL^{-}1$ concentrations, evaluating seed germination tests with ryegrass (*Lolium perenne*), barley (*Hordeum vulgare*) and flax (*Linum usitatissimum*). May *et al.,* (2019) stated that effects of silver nanoparticles (AgNPs) on pea (*Pisum sativum* L.). AgNPs were synthesized by using gelatine/glucose mixture as a reducing/stabilizing agent for silver nitrate. The AgNPs were characterized and their effects on early growth and cytotoxicity on cell division and chromosomes have been studied.

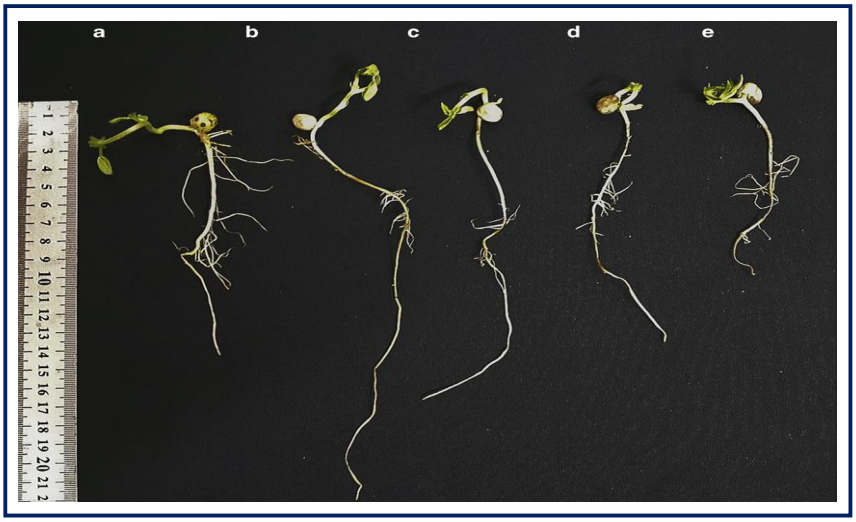

Fig. 19: Illustrates that Seedlings of *Pisum sativum* germinated in different concentrations of silver nanoparticles solutions after 14 days of germination; a control, b 20mg/L, c 40mg/L, d 80mg/L and e 160mg/L.

Seeds of *Pisum sativum* cv. Master B were soaked in AgNPs solutions at concentrations of 20, 40, 80 and 160 mg/L for two hours, control seeds were simultaneously soaked in distilled water. Seeds were then germinated on filter papers moistened with the above concentrations. Seed germination was gradually enhanced at lower concentrations of AgNPs (20 and 40 mg/L) and decreased at higher concentrations (80 and 160 mg/L) compared to control. Seedling growth parameters except root length were all reduced. Deformation of root shape (twisted, folded and hocked roots) was induced upon exposure to AgNPs. Cytosolically, mitotic index declined, and chromosomal abnormalities raised as the concentration of AgNPs increased. Observed abnormalities comprised disturbed mitotic phases and cladistics aberrations such as chromosome bridges, rings, breaks, and micronuclei indicating a genotoxic potential for the AgNPs at high concentrations Fig. (20).

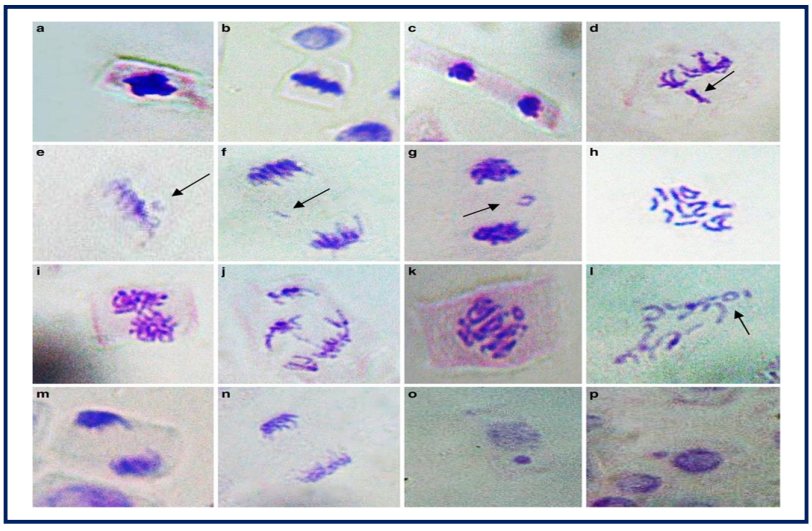

Fig. 20: Illustrates that types of mitotic chromosomal abnormalities induced in pea root tips after treatments with the applied concentrations of AgNPs compared to the control; a–c stickiness in prophase, metaphase and anaphase respectively; d, e unoriented chromosomes in metaphase; f chromosome break at anaphase; g chromosome lagging at anaphase; h C-metaphase; i disturbed metaphase; j chromosome bridge and multipolar cell in anaphase; k , l ring chromosomes at disturbed metaphase; m diagonal anaphase; n unequal distribution in anaphase and o, p micronuclei in interphase. After May *et al.,* (2020)

Results showed that AgNPs at the concentration of 10 mg mL^{-1} had a certain inhibitory effect on germination; however, no trends indicating that smaller particles were more toxic than the larger ones and it seems that, effect were gradually depended on plant species. The absence of concentration and particle size dependant effects observed in this study may be due to saturation or equilibrium being reached, possibly involving an ionic component that was not distinguished in this study El-Temsah and Joner (2012). Toxicity of two types of spherical AgNPs, 6nm AgNP-GA and 21nm AgNP-PVP, as well as of AgNO3 (1, 10 or 40 mg mL^{-1}) seeds of 11 species of wetland plants on the filter paper and in soil was investigated Yin *et al.,* (2012). It was observed that the exposure to 40 mg mL^{-1} AgNP-GA significantly inhibited the germination of *Scirpus cyperinus*, *Juncus effuses* and *Phytolacca Americana*. Moreover, AgNP-GA had more negative effects as compared to $AgNO_3$ suggesting that the high toxicity of AgNP-GA was not only due to the presence of Ag^+, but also as a result of the combination of size, coating and perhaps even surface charge. Moreover, the only significant effect of AgNPs on germination in the soil experiment was inhibition of P. Americana germination after exposure to 40 mg mL^{-1} AgNP-GA Yin *et al.,* (2012), which indicates that the exposure medium also has an influence on AgNPs toxicity. Arabidopsis seeds exposure to 75 and 300 µg mL^{-1} of 20 nm AgNP-citrate, it was found that plants suffered gradual degenerative seed viability with a decreasing germination rate in successive generations Geisler-Lee *et al.,* (2014).; there was no difference in seed germination among E0 generation; however, seed germination rates decreased from the initially exposed (E0) generation through the first (E1) to third (E3) generations exposed to AgNP-citrate. Stronger toxicity of AgNP-citrate as compared to equivalent dosage of $AgNO_3$ was observed Geisler-Lee *et al.,* (2014) Similarly, a 40 nm AgNPs and the same concentration of $AgNO_3$, ranging from 200 to 1600 mg.L^{-1}, were also found to inhibit seed germination of black mustard (*Brassica nigra*) in a dose-dependent manner and the AgNPs also had stronger inhibitory effect than Ag^+ Amooaghaie *et al.,* (20015). These results implicate that AgNPs inhibitory effects observed in germinating seeds are not only due to the dissolved Ag^+ released from AgNPs, but also can be partially attributed to the nanoparticles themselves. However, the results showed that both AgNPs and $AgNO_3$ suppressed lipase activity and reduced the conversion of lipids into soluble and reducing sugars, which led to the decline in oilferous seed germination. Although AgNPs mainly had negative effects on seed germination, there are also some opposite results. Namely, treatment with spherical 30–40nm AgNPs (10, 20 and 30µgm mL^{-1}) accelerated *Boswellia ovalifoliolata* germination; on the solid medium with AgNPs, germination completed within 7–10 days, while for control seeds it took 10–20 days Savithramma *et al.,* (2012) .

Similar results were found after exposure of pearl millet (*Pennisetum glaucum*) seeds to 20 and 50mg mL^{-1} of 13 nm AgNPs Parveen and Rao (2015) Study of Almutairi and Alharbi (2015) on seeds of watermelon (*Citrullus lanatus*), zucchini (*Cucurbita pepo*) and corn (*Zea mays*) treated with 20 nm AgNPs showed that the AgNPs concentrations at which the highest germination rate was observed differed among investigated species; for zucchini it was 0.5 mg. mL^{-1} , for corn 1.5 mg. mL^{-1} and for watermelon 2 mg. mL^{-1} , which indicates that three different crop species had different dose responses to AgNPs in terms of germination. Fayez *et al.,* (2017) reported that although 25nm AgNPs significantly decreased grain germination of barley (*Hordeum vulgare*) when applied in high concentrations (0.5 and 1mM), the lower concentration of 0.1mM positively affected the seed germination. On the other hand, in several studies, exposure to AgNPs did not result with any effects on germination. No effect on germination percentage of flax was observed after exposure to 2, 5 and 20nm AgNPs El-Temsah and Joner (2012). Moreover, AgNPs of different sizes (20, 50 and 65nm) applied in 50 ppm concentration showed no significant effect on seed germination of broad bean (*Vicia faba*) Abdel-Azeem and Elsayed (2013).

The lack of effect on germination was also recorded after exposure of 11 wetland species to AgNP-PVP Yin *et al.,* (2012) , in castor bean (*Ricinus communis*) seeds exposed to AgNP-PVP Yasur and Rani (2013) , in radish (*Raphanus sativus*) seeds treated with colloidal AgNPs Zuverza-Mena *et al.,* (2016) , *Arabidopsis* seeds after treatment with 10nm AgNPs Qian *et al.,* (2013) and after treatment of rocket seeds with 10nm AgNP-PVP Vannini *et al.,* (2013) . From the results of all presented studies, it can be concluded that the susceptibility of plant seeds to AgNPs exposure is more dependent on the plant species than on the physico-chemical characteristics of the particles themselves.

6.2. Effects on plant morphology

Several authors investigated that root morphology of various plant species treated with AgNPs of different sizes, concentrations and coatings show that toxicity effects of roots are the major target by AgNPs treatments. Tripathi *et al.,* (2017), stated that anatomical structures of pea root seedlings grown in Hoagland medium for 15 days revealed that addition of 1000 and 3000µM of biosynthesized 22nm AgNPs, observed that number and length of root hairs was drastically decreased as compared to control. Furthermore, the superficial root cap cells of germinating wheat seedlings, treated for 5 days with 10mg L^{-1} of 10nm AgNP-PVP, undergo degradation, plasmolysis occurs in a greater extent in AgNP- than $AgNO_3$-treated cells; in these cells large vacuoles, and periplasmic space was observed Vannini *et al.,* (2014). Similarly, Yin *et al.,* (2011) found that root tip cells of common grass seedlings failed to develop root hairs, had highly vacuolated and collapsed cortical cells and broken epidermis and root cap after exposure to 40 mg L^{-1} of 6 nm AgNP-GA for 5 days however , seedlings exposed to identical concentrations of $AgNO_3$ showed no such abnormalities.

Moreover, Vannini *et al.,* (2014) reported that in rocket seedlings root tip cells were also more vacuolated after exposure to AgNPs than in the root cells after treatment with $AgNO_3$. Furthermore, in the study of Pokhrel and Dubey (2013), 73.4 µgm L^{-1} of AgNP-citrate (56 nm) and 200 µgm L^{-1} $AgNO_3$ both caused changes in primary root cells at the zone of elongation in 7 days old maize seedlings; cells were consistently elongated after AgNP-treatment, while they appeared thinner and irregular after exposure to $AgNO_3$. On the contrary, light microscopy did not reveal any significant changes in the organization of root apical meristem and elongation zone in the study of tobacco seedlings after 30 days-exposure to 100µM of 50nm AgNP-citrate, while the roots of seedlings treated with the same concentration of $AgNO_3$ were thicker with reduced root cap Peharec *et al.,* (2018) Fig. (21). In several studies, the impact of AgNPs on the seedlings roots was analysed in the organelles at the ultra-structural level by transmission electron microscopy (TEM) Fig. (22). Major changes were observed in plastids, vacuole and endoplasmic reticulum (ER) of root cap, meristems and differentiating cells. The number of the amyloplasts and the size of the smooth endoplasmic reticulum (ER) in the root cap columella cells of rocket seedlings were reduced after both AgNP-PVP- and $AgNO_3$-treatments Vannini *et al.,* (2014). However, only AgNPs induced morphological modifications of ER in the region of cell elongation and differentiation of root samples; in particular, an extensive swelling was observed. In wheat seedlings exposed to AgNP-PVP Vannini *et al.,* (2014), no starch grains were noticed in the root cap columella amyloplasts and in the plastids of meristematic cells.

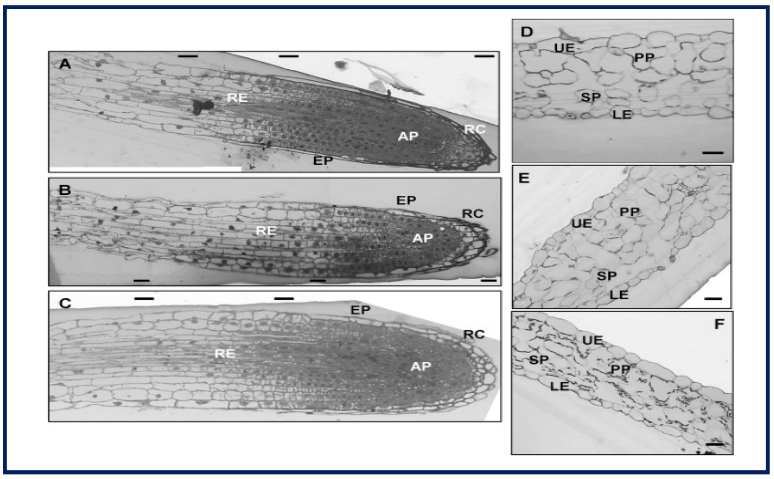

Fig. 21: Semi thin sections of root from (A) control, (B) 100 mM AgNP-treated and (C) 100 mM $AgNO_3$-treated tobacco seedlings (bar ¼ 33.1 mm) and leaf from (D) control, (E) 100 mM AgNP-treated and (F) 100 mM $AgNO_3$-treated tobacco seedlings (bar ¼ 30.6 mm). RC e root cap, AP e apical meristem, RE e region of elongation, EP e epidermis, UE e upper epidermis, LE e lower epidermis, PP e palisade parenchyma, SP e spongy parenchyma. After Peharec *et al.,* (2018)

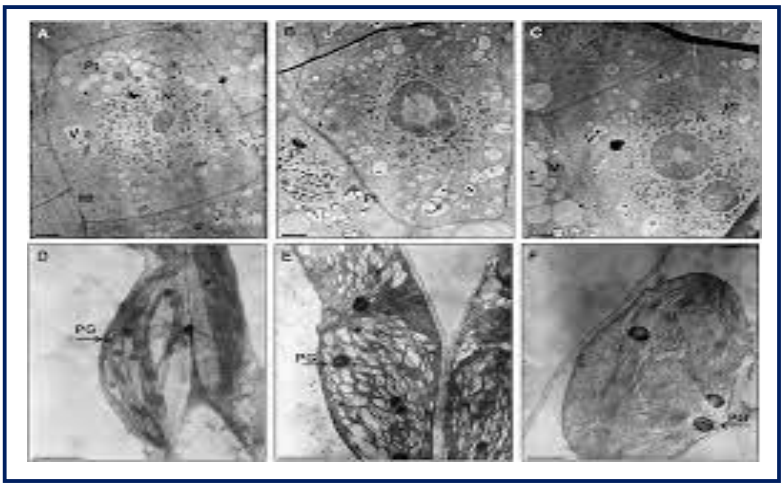

Fig. 22: Ultrastructure of root cells and leaf chloroplasts. Root cells of (A) control, (B) 100 mM AgNP-treated and (C) 100 mM $AgNO_3$-treated tobacco seedlings (bars ¼ 2 mm). Chloroplasts in leaf cells of (D) control, (E) 100 mM AgNP-treated and (F) 100 mM AgNO3-treated tobacco seedlings (bars ¼ 1 mm). N e nucleus, V e vacuole, Mt e mitochondrion, Pt e plastid, PG e plastoglobules. After Peharec *et al.,* (2018)

Peharec *et al.,* (2018) reported that silver nanoparticles (AgNPs) are a dominant nanomaterial in consumer products; there is growing concern about their impact on the environment. Although numerous studies on the effects of AgNPs on living organisms have been conducted, the interaction of AgNPs with plants has not been fully clarified. To reveal the plant mechanisms activated after exposure to AgNPs and to differentiate between effects specific to nanoparticles and ionic silver, we investigated the physiological, ultra-structural and proteomic changes in seedlings of tobacco (*Nicotiana tabacum*) exposed to commercial AgNPs and ionic silver ($AgNO_3$) from the seed stage. A higher Ag content was measured in seedlings exposed to AgNPs than in those exposed to the same concentration of $AgNO_3$. However, the results on oxidative stress parameters obtained revealed that, in general, higher toxicity observed in $AgNO_3$-treated seedlings than in those exposed to nano- silver. Ultra-structural analysis of root cells confirmed the presence of silver in the form of nanoparticles, which may explain the lower toxicity of AgNPs. However, the ultra-structural changes of chloroplasts as well as proteomic study showed that both AgNPs and $AgNO_3$ could affect photosynthesis. Moreover, the majority of the proteins involved in the primary metabolism were up regulated after both. Moreover, the vacuolization increased in the differentiating cells and an extensive swelling was observed in ER, whose tubules appeared packaged in regular structures that occupy a large area of the cell. In this root area the production of a large number of lateral roots primordia was observed, similarly as in wheat roots exposed to AgNPs Dimkpa *et al.,* (2013) Fig. (23).

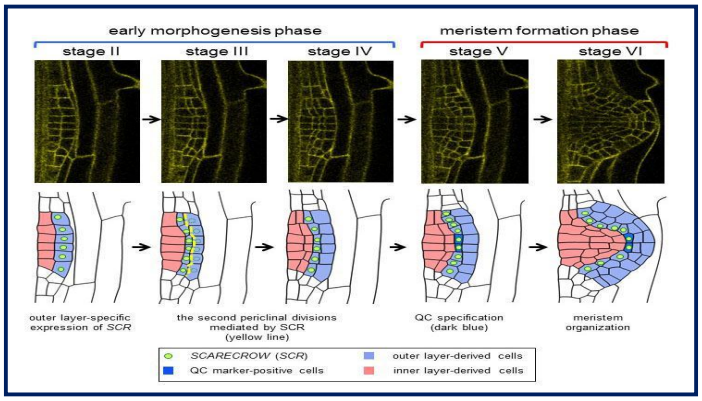

Fig. 23: Illustrates lateral roots grow in this plant, after four layers of primordia are formed, the quiescent center is established, and the meristem is formed.

Lateral root primordium originated very early in the AgNP-PVP exposed root apex and it initiated immediately under the meristematic root apex area in the inner root region. This suggests that AgNPs affect mechanisms controlling lateral root production by the pericycle Vannini *et al.,* (2014), probably by binding of Ag^+ to ethylene receptor McDaniel and Binder (2012) , thus blocking ethylene induced inhibition of lateral root production usual for dark-grown seedlings. Since in both studies by, Vannini *et al.,* (2014), it was demonstrated by TEM that AgNPs did not enter the root cells, while some electron-dense spots were associated with the cell walls of outer root tip cells, it has been suggested that primarily Ag^+ released from NPs at the root interface mediates the effects of AgNPs. However, there are some investigations showing that observed morphological effects of AgNP exposure could be a result of the immediate uptake of AgNPs by root cells. Beside changes in root cells, AgNPs also induce morphological modifications in the leaves of seedlings of various plant species. Tripathi *et al.,* (2017) reported that leaf chloroplasts in mesophyll cells, proto-xylem, meta-xylem and phloem of pea seedlings exposed to AgNPs (1000 and 3000µM) were adversely affected. After exposure to 3000 µM, AgNPs mesophyll tissue was not differentiated into palisade and spongy parenchyma cells, while lower epidermal cells of the leaf midrib were more elongated compared to treatment with 1000µM AgNPs. On the contrary, in the study of Peharec *et al.,* (2018) leaf anatomy showed no significant changes in the cell organization of tobacco seedlings exposed to 100 µM AgNP-citrate compared to the control; however, leaves of seedlings treated with 100 µM $AgNO_3$ were thinner with bigger chloroplasts. In several studies the impact of AgNPs on leaves of exposed seedlings was also analysed at the Ultrastructural level and TEM studies revealed changes primarily in the chloroplasts; disturbances in their shape, thylakoid system, plastoglobules and the starch content were observed Fig.(24). Chloroplasts in the needles of old Scots pine (*Pinus sylvestris*) seedlings, treated by spraying seedlings aerial parts with 50 ppm of AgNPs, have been modified from lenticular to round Aleksandrowicz-Trzcinska *et al.,* (2018), while chloroplasts of English oak (*Quercus robur*) seedlings, also treated by spraying with the same AgNPs, contained large starch granules Olchowik *et al.,* (2017).

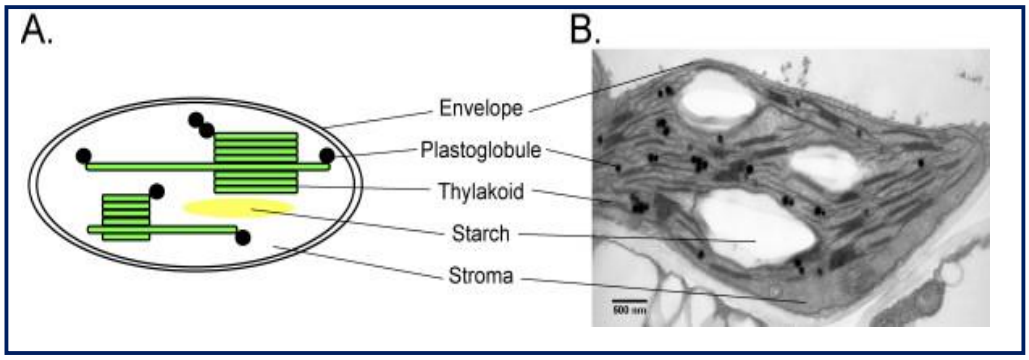

Fig. 24: Illustrates plastoglobules lipoprotein particles in chloroplasts. **A**. Schematic diagram of a chloroplast. The organelle is delimited by a double membrane system (envelope). The interior of chloroplasts comprises the aqueous stroma, the thylakoid membranes (green) and starch granules (yellow). Plastoglobules (black circles) are lipid particles associated with thylakoids. **B.** Transmission electron micrograph of an Arabidopsis chloroplast. Plastoglobules are visible as dark round bodies after post fixation with osmium tetroxide.

In the leaves of 100 µM AgNP-citrate treated tobacco seedlings, chloroplasts were swollen with dilated thylakoid systems and bigger plastoglobules than the control; chloroplasts in seedlings exposed to 100 µM$AgNO_3$ showed similar changes as those found after AgNP-exposure Peharec *et al.,* (2018). These results are partially in agreement with those reported by Qian *et al.,* (2013), where 3 mg L^{-1} of both 10 nm AgNPs and Ag^+ reduced cell size and disrupted the thylakoid membrane structure in Arabidopsis seedlings; however, the impact on chloroplast ultrastructure was less pronounced in $AgNO_3$-treated seedlings. In general, chloroplasts were shown to be the most sensitive organelles in the leaves of seedlings of different plant species exposed to AgNP-induced stress. Morphological modifications and ultra-structural changes of roots, stems and leaves were also observed in the fully developed stage of various plant species. In *A. cepa*, the highest applied AgNP concentration of 100ppm

induced complete disintegration of cell walls for most of the cells Kumari *et al.,* (2009). Anatomical investigations of the transverse sections of *Bacopa monnieri* roots exposed to AgNPs in 10 ppm concentration showed disappearance of the characteristic air chambers and partition filaments in root cortex, although the same observations were obtained after exposure to 10ppm $AgNO_3$ Krishnaraj *et al.,* (2012).

In the same study, light microscopy analysis also revealed structural aberrations in the stem anatomy including alterations of shape, size and distribution of xylem elements, after both silver treatments. In the study of Cvjetko *et al.,* (2018), microscopic analyses showed that the root tip cells of tobacco adult plants were highly vacuolated after 7 days of exposure to both 100 μM AgNP-citrate and $AgNO_3$. Furthermore, TEM study showed that after both types of treatments only nuclei could be observed within the root cells, due to large vacuoles; however, exposure to $AgNO_3$ also resulted with partly destroyed root cells, while nuclei were highly damaged Cvjetko *et al.,* (2018). In the same study, AgNPs were detected in the intermembrane space of the root cells, which proves their direct uptake and accumulation in the root cells Cvjetko *et al.,* (2018). In the study of tobacco plants exposed to AgNPs, leaf semi thin sections showed no significant changes in the cell organization, except for the difference in the leaf thickness were the leaves of AgNP-treated plants were thinner than the control ones Cvjetko *et al.,* (2018). Moreover, Fayez *et al.,* (2017) reported that the leaf chlorosis of barley plants exposed to 25nm AgNP or $AgNO_3$ appeared after 7–12 days, which was dependent on the dose and type of treatments, although leaf chlorosis was more evident after treatments with $AgNO_3$ than with AgNPs. Furthermore, analysis of leaf ultrastructure showed destruction of chloroplasts, mitochondria and nucleus after both types of treatments. Namely, in response to 1mM AgNPs, chloroplasts had few small plastoglobuli and well defined grana thylakoids and stroma lamellae, although a reduction in size of grana thylakoids to stroma lamellae was observed; additionally, nuclear envelope was ruptured.

After exposure to 1m M $AgNO_3$ opposite effects were recorded; chloroplasts were characterized with big plastoglobuli, condensed stroma matrix, formation of vesicles and dilated grana thylakoids, while stroma lamellae lost their organization Fig, (24). Moreover, the mitochondrial envelope and cristae were partially or very degenerated and in the nucleus clumping of nuclear chromatin into more densely packed material was observed Fayez *et al.,* (2017). In duckweed *S. polyrhiza*, ultra-structural changes in chloroplasts were observed after 72h of exposure to 6nm AgNP-GA and 20nm AgNP-PVP (10 mg L^{-1}); chloroplasts were characterized with accumulated starch and large starch grains as well as with fewer intergranal thylakoids Jiang *et al.,* (2014). In leaf cells of tobacco plants, chloroplasts were smaller and somewhat swollen and ruptured, although with well-developed thylakoid system after exposure to AgNP-citrate, while those found in cells of $AgNO_3$-treated plants were bigger than in the control Cvjetko *et al.,* (2018). Ultra-structural damage of chloroplasts, mitochondria and nucleus found in abovementioned studies confirms that these organelles are the main targets affected by AgNPs, although chloroplasts were shown to be the most sensitive organelles Fig. (25).

In conclusion, the impact of AgNPs on seed germination and growth, morphology and ultra-structural of plants depends on various AgNP characteristic such as size, chemical composition, surface structure and oxidative dissolution. Their influence also seems to depend on the plant species and growth stage of plant, the type of substrate (soil or different nutrient media) the concentrations of nanoparticles involved and the manner of the application (foliar or soil). After AgNP accumulation in plants, they generally start degrading the quality of plants with generally negative impact on the root growth of germinating seedlings and the fresh biomass of the plant through the reduction in root elongation and biomass. Since roots are the first target tissue to confront with AgNP solution, toxic symptoms appear more in roots rather than in shoots, but AgNPs also induce morphological modifications in the stem and leaves. The main cell targets affected by AgNP toxicity are chloroplasts, mitochondria and nucleus, although there is still an open debate is the toxicity caused by AgNPs themselves or released Ag^{+}.

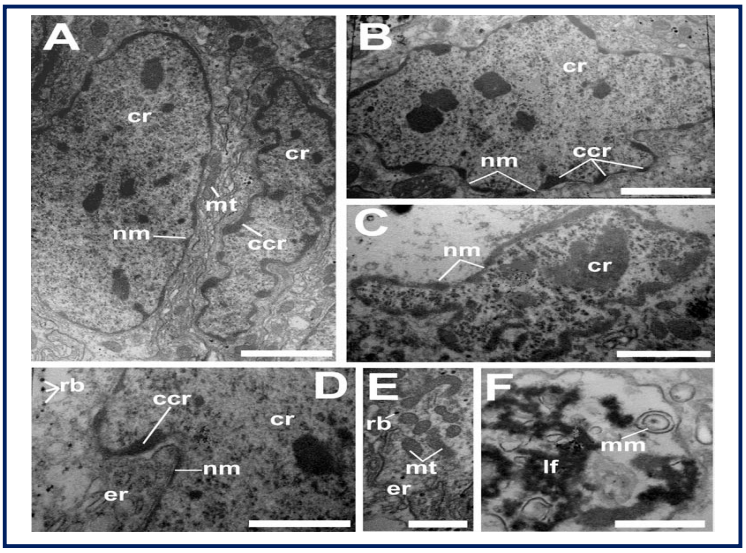

Fig. 25: Illustrates ultra-structural of nuclei and organelles. A: Nucleus of a viable (left) and an apoptotic (right) gland cell. cr: chromatin, nm: nuclear membranes, ccr: peripheral condensation of chromatin, mt: mitochondria, bar: 1 µm. B-C: Serrated and segmented nuclei of apoptotic cells. Bars: 1 µm. D: Nuclear membranes of a serrated nucleus. cr: chromatin, ccr: condensed chromatin structures, nm: nuclear membranes, er: endoplasmic reticulum, rb: polyribosomes. Bar 20 nm. E: Mitochondria and endoplasmic reticulum of an apoptotic gland cell. rb: ribosomes, mt: mitochondria, er: endoplasmic reticulum, bar: 10 nm. F: Lipofuscine granules (lf) and multilayered membrane structures (mm) in an apoptotic gland cell. Bar is 30 nm.

7. Effects on photosynthesis

Photosynthesis is a key process for life on Earth in which plants and other photosynthetic organisms, like algae and cyanobacteria, change light energy into chemical energy Fig. (26).

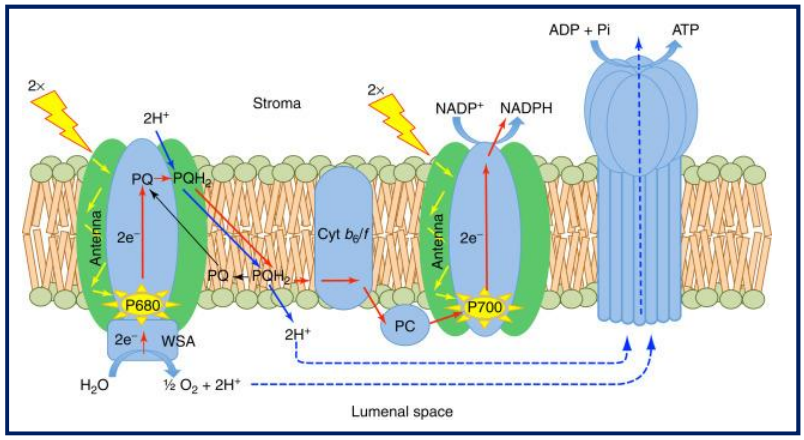

Fig. 26: Illustrates photosynthetic electron transport.

Photosynthesis represents a major physiological process for the maintenance of cellular viability and growth. Photosynthetic process is known to be very sensitive to stress caused by adverse environmental conditions, such as high light, drought, salinity, heat and heavy metals Murchie and Lawson (2013). A decrease in chlorophyll content as a parameter of AgNP phytotoxicity has been noticed in various organisms including marine and freshwater microalgae Miao *et al.,* (2009), Oukarroum *et al.,* (2012), and Oukarroum *et al.,* (2012). Aquatic plants Zou *et al.,* (2017) , Jiang *et al.,* (2012) , Jiang *et al.,* (2017) , crop plants Tripathi *et al.,* (2017), Tripathi *et al.,* (2017),, Vishwakarma

et al., (2017) , Das *et al.,* (2018), Nair and Chung (2018), Pardha-Saradhi *et al.,* (2018) as well as a model plant *Arabidopsis*

Ke *et al.,* (2017), Nair Chung *et al.,* (and 2014), Qian *et al.,* (2013), Sosan *et al.,* (2016). Beside chlorophyll content, chlorophyll a fluorescence has been proposed as a sensitive, non-destructive, rapid, and efficient method for detecting the impacts of environmental stress on photosynthetic efficiency Krause and Weis (1991), Strasser *et al.,* (2004). Light energy absorbed by chlorophyll molecules can be used for photochemistry, be re-emitted as heat or be re-emitted as fluorescence. Since these three processes are in competition with each other, the yield of chlorophyll fluorescence emission gives us valuable information about the quantum efficiency of photochemistry, which is responsible for providing energy and reducing power for CO_2 assimilation. The analysis of changes in chlorophyll fluorescence kinetics provides detailed information on the structure and function of the photosynthetic apparatus and various parameters derived from fluorescence measurement data have been widely used as sensitive biomarkers of phytotoxic effects Strasser *et al.,* (2004). Several authors evaluated AgNP phytotoxicity by measuring different fluorescence parameters, most often maximum quantum yield (Fv/Fm) of photosystem II (PSII), which corresponds to the efficiency by which an absorbed photon will be trapped by PSII reaction centers Krause and Weis (1991), and found that PSII efficiency in various algae and plants was significantly reduced after AgNP exposure Tripathi *et al.,* (20178),, Tripathi *et al.,* (2017), Jiang *et al.,* (2012), Jiang *et al.,* (2017). The change of fluorescence parameters under a light adapted state, which can provide information about the efficiency of photochemical reactions and/or heat dissipation of chlorophyll excitation energy, has also been analysed Vishwakarma, *et al.,* (2017), Jiang *et al.,* (2012), Dewez and Oukarroum (2012) , Shabnam *et al.,* (2017). More recently, a measurement of rapid fluorescence induction curves with high resolution and the parameters of the so-called JIP-test have been used to assess the behavior of various components of photosynthetic apparatus in plants and algae exposed to AgNPs Oukarroum *et al.,* (2012), Pardha-Saradhi *et al.,* (2012), Dewez and Oukarroum (2012), Shabnam *et al.,* (2017), Matorin *et al.,* (2013).

Misra *et al.,* (2008) stated that light energy is absorbed by chlorophyll, carotenoids and other pigment molecules present in the photosynthetic antenna molecules present in the thylakoid membranes of green plants Strasser *et al.,* (2000), (2004); Govindjee, (2004); Maxwell and Johnson, (2000); Falkowski and Raven, (2007). Absorption of a photon raises a chlorophyll *a* molecule to its lowest singlet excited state, for which three internal decay pathways exist: fluorescence, in which the molecule returns to the ground state with the emission of radiation; internal conversion, in which the energy of the molecule is converted into vibrational energy; and intersystem crossing, in which the singlet state is converted to the triplet state Fig. (27).

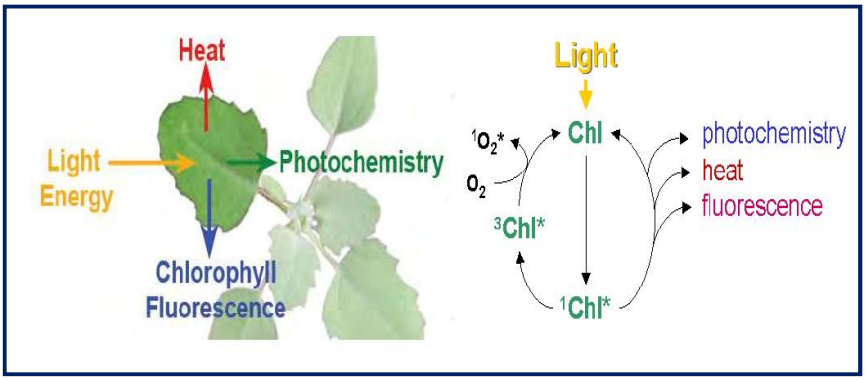

Fig. 27: Illustrates the origin of chlorophyll fluorescence: basic aspects. After Misra *et al.,* (2008)

If certain other molecules are present along with the chlorophyll, external decay pathway(s) may also become available in addition to the internal decay pathways. Such external pathways facilitate the transfer of energy to a molecule with a similar energy gap or the transfer of an electron to or from another molecule, such as in excitation energy transfer in light-harvesting antennae and charge separation in photochemical reaction centers, respectively. All of these downward processes competitively contribute to the decay of the chlorophyll-excited state. Accordingly, an increase in the

rate of one of these processes would increase its share of the decay process and lower the fluorescence yield (φf). The quantum yield of chlorophyll fluorescence from the photosynthetic apparatus is therefore 0.6-3%, while chlorophyll *a* in an organic solvent exhibits a high fluorescence yield of approximately 30% Latimer *et al.,* (1956); Trissl *et al.,* (1993). Oxygenic photosynthesis is endowed with the unique property of a fluorescence emission. Light energy that is absorbed by chlorophyll in photosynthetic systems can undergo three fates: a) it can be used to drive photosynthesis (photochemistry), b) it can be dissipated as heat or c) it can be re-emitted as red fluorescence. These three processes occur in competition. Since the sum of rate constants is constant, any increase in the efficiency of one process will result in a decrease in the yield of the other two. Therefore, determining the yield of chlorophyll fluorescence will give information about changes in the efficiency of photochemistry and heat dissipation.

Toxicity of AgNP at the physiological level is predicted by reduction in chlorophyll content, decline in nutrient uptake, reduction in the rate of transpiration, and alterations in hormonal activities Yan and Chen (2019). ROS and lipid peroxidation reaction were seen to be increased in AgNP treated plants, which were shown to inhibit photosynthetic pathways under elevated concentrations Dewez and Oukarroum (2012). Accumulation of Ag and severe inhibition in photosynthesis was observed in seedlings of *Brassica sp.* after exposure to AgNP Vishwakarma *et al.,* (2017). Olchowik *et al.,* (2017) also observed that plants treated with AgNP exhibited a disturbed ultrastructure of leaves, especially, in the photosynthetic apparatus. Contradictorily to this, Farghaly and Nafady (2015) and Latif *et al.,* (2017) observed that AgNP signifcantly promoted photosynthesis, which was closely related with change in the rate of nitrogen metabolism Fig. (28).

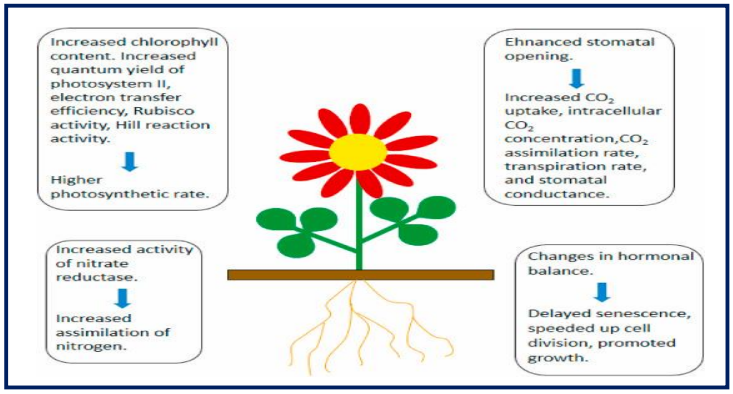

Fig. 28: Positive effects of nanoparticles on plant growth and development. The optimum concentration of nanoparticles causes an alteration in different physiological processes to increase seed germination and photosynthesis of the plants.

Silver NPs can affect the photosynthesis adversely by disturbing the synthesis of chlorophyll. Exposure of Skeletonema costatum to AgNP decreased the cell viability and chlorophyll content due to an excess of ROS Huang *et al.,* (2016).

Nanomaterials have gained exceptional arrays in the field of agriculture, environment, and health Hossain *et al.,* (2015); Mapara *et al.,* (2015), Patil *et al.,* (2016); Kumar *et al.,* (2018) and have significant applications in biomedicines, electronic devices, and biosensors Ma *et al.,* (2015). The highly reactive property of NPs Ghosh *et al.,* (2016) results in increased toxicity through different mechanisms. Therefore, highly reactive nature allows them to easily penetrate into cells, thus causing possible nanotoxicity to living organisms like animals, microorganisms, and plants. Thus, ever-increasing synthesis of nanoparticles in different fields has raised the risks of environmental exposure Ghosh *et al.,* (2016). The agricultural area is facing a higher risk of their exposure, particularly, to engineered nanoparticles Kohli *et al.,* (2019)). Nanoparticles released in the environment by various processes may interact with plants causing many morphological, anatomical, physiological, and genetic changes Fig. (29).

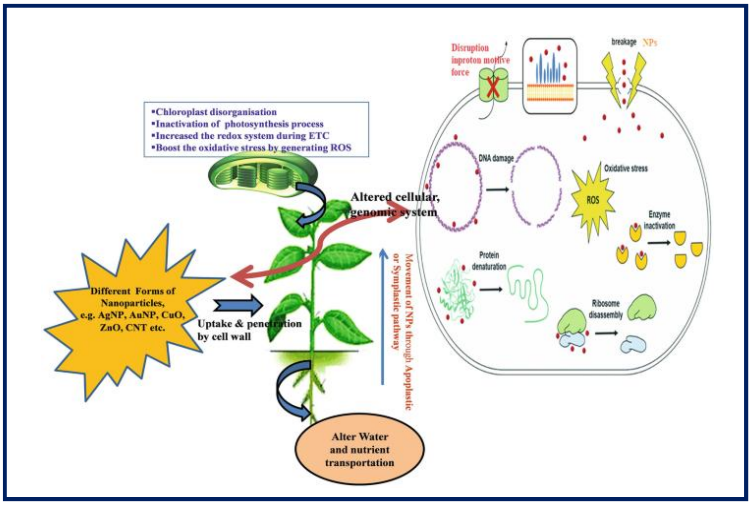

Fig. 29: An overview on nanoparticle interaction in plant system and their phytotoxic effects at all stages of plant development

Similarly, Nair and Chung (2014) and Al-Huqail *et al.,* (2018) demonstrated decreased chlorophyll and carotenoids, shoot-root elongation, fresh weight and protein in *Oryza sativa* and *Lupinus termis* seedlings, respectively, after exposure to AgNP. Contradictorily, Racuciu and Creange (2007) reported that chlorophyll of *Zea mays* increased with low concentration of AgNP treatment while declined in response to higher concentration of it. Higher content of photosynthetic pigments, that is, chlorophylls and carotenoids, would increase the rate of photosynthesis, due to which there was more synthesis of photosynthetic products, which in turn increased the weight and growth of plant. Similarly, Govorov and Carmeli (2007) observed an induction in chemical energy production in photosynthetic systems due to the metal NPs.

8. Chloroplast Membrane

Chloroplasts are responsible for photosynthetic conversion of CO_2 to carbohydrates. In addition, they synthesizes amino acids, fatty acids, and the lipid components of their own membranes. Moreover, these are only one of the several types of related organelles (plastids) that play a variety of roles in plant cells. Plant chloroplasts are large organelles, bounded by a double membrane called the chloroplast envelope. In addition, chloroplasts have a third internal membrane system, called the thylakoid membrane. The thylakoids are formed by membrane network of fattened discs, which are subsequently arranged in stacks called grana. In leaves of *Arabidopsis thaliana*, AgNP caused disruption in membranous structure of thylakoid and decreased the chlorophyll content, and ultimately terminated the plant growth Qian *et al.,* (2013). Similar alterations in thylakoids, decline in chlorophyll, and disruption in essential elements of Physcomitrella patens were documented by Liang *et al.,* (2013) in response to AgNP. Moreover, Olchowik *et al.,* (2017) observed small plastoglobules on chloroplasts of non-treated *Quercus robur*, whereas larger starch granules in AgNP treated leaves.

Aleksandrowicz-Trzcinska ´nska (2019) reported that metal nanoparticles (MNPs) are finding ever-wider applications in plant production (agricultural and forestry-related) as fertilisers, pesticides and growth stimulators. This makes them essential to examine their impact on a variety of plants, including trees. In the study detailed here, we investigated the effects of nanoparticles of silver and copper (i.e., AgNPs and CuNPs) on growth, and chlorophyll fluorescence, in the seedlings of *Scots pine* and *Pedunculate oak*. Fig. (30) We also compared the ultra-structure of needles, leaves, shoots and roots of treated and untreated plants, under transmission electron microscopy. Seedlings were grown in containers in a peat substrate, prior to the foliar application of NPs four times in the course of the growing season, at the four concentrations of 0, 5, 25 and 50 ppm. We were able to detect species-specific activity of the two types of NP. Among seedling pines, the impact of both types of NP at the concentrations supplied limited growth slightly. In contrast, no such effect was observed for the oaks grown in the trial. Equally, it was not possible to find Ultra-structural changes in stems and roots

associated with the applications of NPs. Cell organelles apparently sensitive to the action of both NPs (albeit only at the highest applied concentration of 50 ppm) were chloroplasts. The Cu-NP treated oaks contained large plastoglobules, whereas, those dosed with AgNP contained large starch granules. The NP-treated pines likewise exhibited large numbers of plastoglobules, while the chloroplasts of NP-treated plants in general presented shapes that changed from lenticular to round. In addition, large osmophilic globules were present in the cytoplasm. Reference to maximum quantum yields from photosystem II (Fv/Fm) because of chlorophyll a fluorescence measurements revealed a slight debilitation of oak seedlings following the application of both kinds of NP at higher concentrations. In contrast, in pines, this variable revealed no influence of AgNPs, as well as a favourably affect due to the CuNPs applied at a concentration of 5 ppm. Our research also showed that any toxic impact on pine or oak seedlings due to the NPs was limited and only present with higher concentrations.

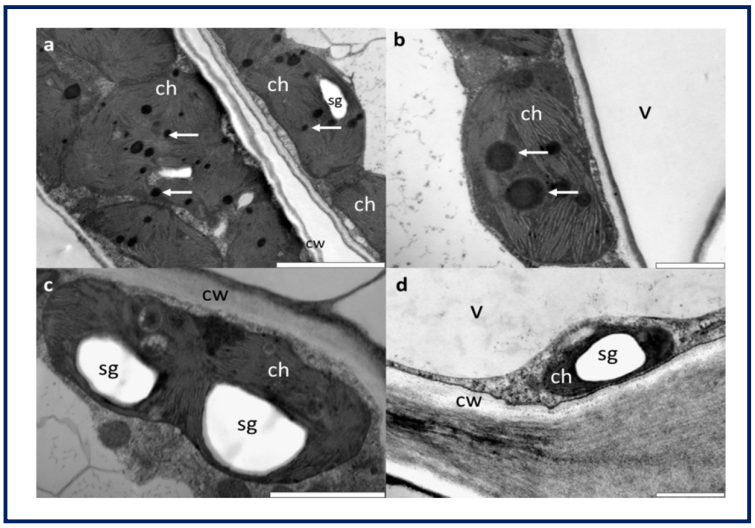

Fig. 30: Illustrates ultrastructure of oak leaves under TEM. (a) Cross-section of palisade mesophyll cells in control oak leaf. (b) Plant treated with 50 ppm CuNPs—chloroplast with disturbed ultrastructure, large plastoglobules. (c,d) Chloroplasts from plants treated with 50-ppm AgNPs containing large starch granules. Abbreviations: cw—cell wall; ch—chloroplast; sg—starch granule; v—vacuole; white arrow—plastoglobule. Scale bars: a = 5 µm, b = 1 µm, c = 2 µm, d = 1 µm. After Aleksandrowicz-Trzcinska ´nska (2019).

8.1. Stomatal Conductance

Stomata are microscopic pores in plant epidermis surrounded by a pair of guard cells. Opening and closure of stomatal pore is regulated by change in guard cell turgor pressure. Reactive oxygen species are important signals involved in the regulation of stomatal movement Song *et al.,* (2014) Murata *et al.,* (2015). Regulation of stomatal aperture requires coordinated functioning of ROS-generating enzymes, signaling proteins, and downstream executors such as ion pumps, transporters, and plasma membrane channels that control guard cell turgor pressure Sierla et al., (2016). Stomatal opening can be promoted by activation of plasma membrane H^+- ATPase. Researches on well-known components including blue light receptors and plasma membrane H^+-ATPase regulating light-induced stomatal opening showed AHA2 to be the major gene related to the stomatal opening process. However, accumulation of ROS in the apoplast and chloroplasts is among the earliest hallmarks of stomatal closure Kim *et al.,* (2015). During AgNP treatment, ROS accumulation directs the changes in gene expression and stomatal closure, with subsequent decline in the rate of transpiration, gaseous exchange, and water loss Mattila *et al.,* (2015). Due to the AgNP-induced stomatal closure, remarkable decline in the rate of transpiration was observed in *Cucurbita pepo* Hawthorne *et al.,*) 2012).

A cascade of signaling network stomata are broadly known for mediating photosynthetic CO_2 exchange and for the efficient use of water for generating the transpirational pull for the ascent of sap Song *et al.,* (2014) Fig. (31).

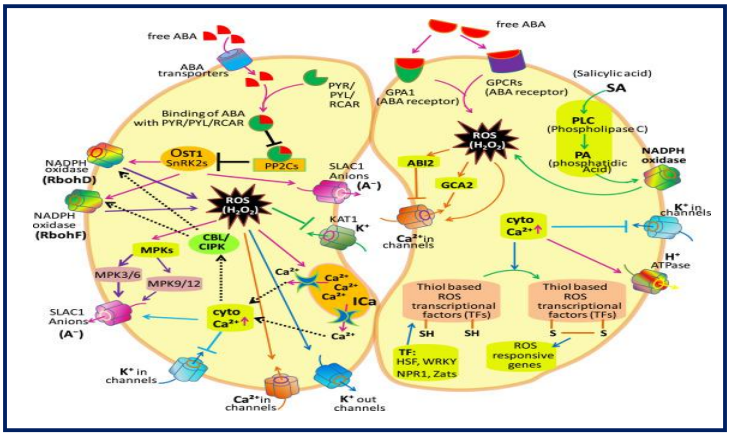

Fig. 31: Targets of reactive oxygen species (ROS) in guard cells. The ROS with sensors play a key role in stomatal movement, which not only supervise ROS concentration in and out of the cell, but also respond to ROS signals. Here the abbreviations are; different channels: NADPH oxidase channels (RbohD and RbohF); S-type anion channel; SLAC1; calcium channels (Ca^{+} in), potassium channels KAT1 (K+ in channel), etc. Receptors; G protein-coupled receptor (GPCR); ABA receptor (PYL/PYL/RCAR); type 2C protein phosphatase (PP2C); open stomata 1 (Ost1); Sucrose nonterminating-related protein kinase 2 (SnRK2s); Arabidopsis α-subunit of the trimeric G protein (GPA1). Calcium dependent protein kinase; MPK, mitogen activated protein kinase (MPK3/6, MPK9/12); Growth Controlled by Abscisic Acid 2 (GCA2); ABA insensitive 2 (ABI2); Ca^{2+}-permeable (ICa); Calcineurin-B Like Proteins (CBLs) proteins; CBL Interacting Protein Kinases (CIPKs), transcriptional factors; HSFs, heat shock transcription factors; Zats, zinc finger proteins; WRKYs, WRKY transcription factors; NPR1, nonexpressor of pathogenesis-related genes 1 After Song *et al.,* (2014), Singh *et al.,* (2017).

Stomatal pore size is regulated by guard cells through a combination of environmental and endogenous signals that affect stomatal movement Kim *et al.,* (2010), Misra *et al.,* (2015). Stomatal movement mediated by ROS has created tremendous interest in their signaling mechanisms as well as network. Each network has unique and distinct receptors and early signaling elements but they also have common components, for instances, plasma membrane anion channels and K^{+} channels through which solute fluxes drive water influx/efflux during actual stomatal movement. ROS are reported as vital participants in guard cell signaling; in particular, H_2O_2 plays a key role in ABA -induced stomatal closure Suzuki *et al.,* (2013) Mittler and Blumwald (2015). Water stress is a common symptom of plants growing in dry soil, as water lost from leaves surpasses the amount taken up by the roots and leads to cellular dehydration, damage, and finally death. Cellular dehydration also occurs, when plants are exposed to other abiotic stresses that limit water supply, such as anaerobic conditions resulting from root flooding or cold and salt stress. Under water stress condition, plants close their stomata as a defence response in order to minimize the loss of water, and the stomatal movement during this stress is regulated by redistribution and synthesis of ABA. ABA alters the gene expression that controls other ameliorative responses such as the maintenance of root water uptake, synthesis of osmoprotectiv proteins, and various metabolic changes Zhu (2002), Seki *et al.,* (2007). Oxidative stress is a common characteristic of various abiotic stresses which disturbs the redox balance of cell thereby increasing the ROS production that are controlled either by antioxidant enzymes or by reaction with antioxidant molecules. The phytohormone ABA is synthesized in shoots, roots, and particularly in seeds, veins and guard cells Boursiac *et al.,* (2013) and plays an important role in various physiological processes, such as development and the regulation of stomatal function in response to abiotic stresses. In case of high salinity and water stress, ABA starts to accumulate in the plant cell and its accumulation directs the changes in gene expression and stomatal closure, with subsequent decrease in transpiration and water loss Shinozaki and Yamaguchi-Shinozaki (2007).

Gaseous exchange decreases as an outcome of stomatal closure thereby resulting into decrease in photosynthetic activity Song *et al.,* (2014), Ma *et al.,* (2009). Under stress conditions, ABA

concentration increases due to release from its conjugated forms or enhanced biosynthesis and decreased degradation. These steps taking place within the affected cell or in neighboring cells results in uptake of ABA by non-stressed cells; ABA in cells is sensed by the ABA receptors. The regulatory network of ABA involves three major components of ABA receptor; the PYRABACTIN (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR; i.e., PYR/PYL/RCAR Ma *et al.,* (2009), Joshi-Saha *et al.,* (2011) , a type-2C protein phosphatase (PP2C; a negative regulator), and a SNF1-related protein kinase 2 (SnRK2; a positive regulator). These component shows a double negative regulatory system (PYR/PYL/ RCAR—|PP2Cs; PP2Cs —|SnRK2) Klingler *et al.,* (2010), Umezawa *et al.,* (2010). In guard cells, ABA is sensed by PYL/PYR/RCAR (PYLs), which binds to ABA. PYLs change their conformation and then interact and inhibit PP2Cs. PP2Cs interact with Sucrose-Non-Fermenting Kinase 1 (SNF1)-related SnRK2s protein kinase open stomata 1 (OST1), leading in dephosphorylation of Ser/Thr residues present at the activation loop of the SnRK2s, resulting in its inactivation Zhang *et al.,* (2015). Therefore, it is concluded that ABA interacts with PYLs complex, inactivates the inhibitory function of PP2Cs, and activate SnRK2 protein kinase OST1 Klingler *et al.,* (2010), Umezawa *et al.,* (2010). Activated OST1 directly binds with and phosphorylates SLOW ANION CHANNEL-ASSOCIATED1 (SLAC1), the anion channel that mediates the release of anions from guard cells, promoting stomatal closure Umezawa *et al.,* (2010), Brandt *et al.,* (2012). OST1 also interacts and phosphorylates with plasma membrane-bound N terminus of respiratory burst oxidase homolog D (RBOHD) and F (RBOHF) protein and in the guard cells of ost1 knockout mutant, the ABA-induced ROS generation is eliminated thereby suggesting that OST1 catalyzes ROS production (H_2O_2) mediated by NADPH oxidase Umezawa etal (2010), Brandt *et al.,* (2012).

Recently, Shi *et al.,* (2015) reported that OST1 compromised the CO_2-induced H_2O_2 and NO accumulation, upregulation of SLAC1 expression, and reduced stomatal aperture. Kwak *et al.,* (2003) have reported that H_2O_2 application in guard cells activates ABA-mediated activation of the hyperpolarization-regulated Ca^{2+}- permeable (ICa) channels and produces concurrent cytosolic Ca^{2+} increase, and this activation was found to be damaged in the ABA insensitive gca2 mutant. The plasma membrane-bound anion channels that are activated by elevated cytosolic Ca^{2+} concentrations cause a membrane depolarization resulting to the hang-over of inward K+ KAT1 channels Osakabe *et al.,* (2014). Upon Ca^{2+} binding, CALCINEURIN-B LIKE PROTEINS (CBLs) interact and regulate the CBLINTERACTING PROTEIN KINASES (CIPKs) activity Luan *et al.,* (2009). CBL1/CBL9-CIPK26 complex interact and phosphorylates RBOHF, which is located at the plasma membrane thereby suggesting that CIPK26-mediated RBOHF regulation occurs at the plasma membrane and not by the CBL-CIPK dependent translocation regulatory mechanism Luan *et al.,* (2009) , Drerup *et al.,* (2013) . Further, the Ca^{2+}-CBL-activated kinase i.e. CIPK26 mediated phosphorylation of RBOHF resulted in enhanced ROS production Drerup *et al.,* (2013) . Several works have suggested that apoplastic ROS accumulation actively participates in the initiation of stomatal closure An *et al.,* (2008), Khokon *et al.,* (2011) . According to Okuma *et al.,* (2008) reduced glutathione (GSH) concentrations decreases by increasing ABA levels in guard cells and in GSH knockout mutants enhanced ABA-induced stomatal closure was observed. In cad2-1 mutant of *A. thaliana* lacking gamma-glutamylcysteine synthase (catalyzes the first step in GSH biosynthesis), an increase in H_2O_2 level by the hyperpolarized-activated Ca^{2+} channel in plasma membrane of the guard cell was observed along with an increase in H_2O_2-induced stomatal closure Munemasa *et al.,* (2013). As the cytosolic GSH in the guard cell was induced by ABA and not by H_2O_2, it had been suggested that apoplastic ROS signal might alter the responsiveness of the guard cells to ABA by stimuli other than ABA itself Okuma *et al.,* (2008), Munemasa *et al.,* (2013), but this view has not been experimentally evidenced so far. ROS are suggested to elevate the free ABA levels either by enhancing ABA biosynthesis or by inhibiting ABA degradation Song *et al.,* (2014) Boursiac etal (2013), Daszkowska-Golec and Szarejko (2013).

Therefore, increased ROS levels might result into increased ABA accumulation while increased ABA might results into increased ROS generation thereby forming a positive feedback loop in mediating stomatal closure. It is commonly known that ROS (such as O_2 •− and H_2O_2) and NO are produced in response to similar stimuli and with similar kinetics. In the leaves of *Phaseolus aureus*, exogenous H_2O_2 triggered NO ssgeneration in the guard cells Lum *et al.,* (2002) . Neill *et al.,* (2008) who reported that nitric oxide synthase (NOS) as well as nitrate reductase (NR) both are necessary for ABA-induced NO generation in the guard cell of *Arabidopsis* supported these findings. NO induces

MAPK activity, cGMP, and Ca^{2+} production that are vital for ABA-induced stomatal closure under stress conditions Neill *et al.,* (2008). ABA and H_2O_2 can directly participate in stomatal closure via NO-independent signaling.

For instance, in order to struggle with increased ROS, superoxide dismutase (SOD) activity might increase along with the ascorbate peroxidase (APX) and catalase (CAT), and dehydrin like proteins can be produced in order to improve the effects of cell dehydration Neill *et al.,* (2008) Fig. (32).

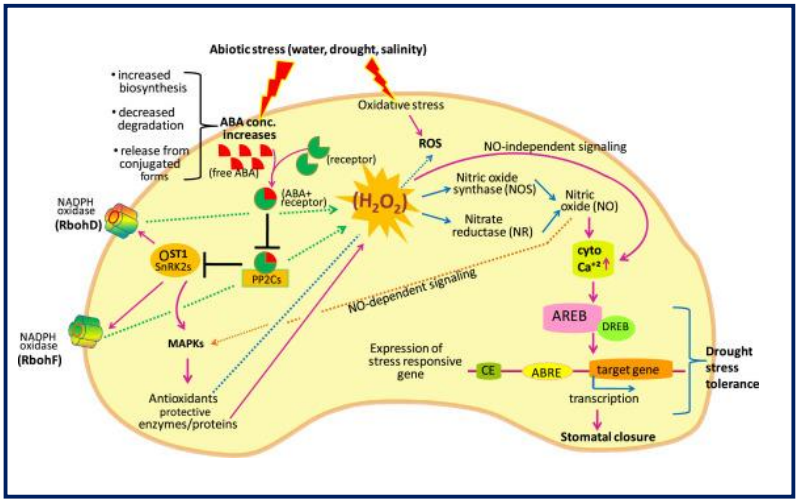

Fig. 32: During stress condition, ABA accumulates in the guard cells via different ways. It enters into guard cells via ABA transporters, synthesized in response to signals like increased ROS, or accumulates as a result of decreased degradation or release of ABA from conjugated sources. The accumulated ABA interacts with the PYR/PYL/RCAR receptor, and inhibits the PP2Cs, which will result into activation of OST1 and phosphorylation and activation of NADPH oxidase (Rboh). NADPH oxidase facilitates H_2O_2 generation via signaling pathway·H_2O_2 induces NO generation by nitric oxide synthase (NOS)-like enzyme(s) and nitrate reductase (NR) that result in the opening of ROS-regulated Ca2+ channels. NO enhances antioxidant gene and enzyme activity via MAPK signaling pathways. H_2O_2 directly induces ROS-regulated Ca^{2+} channels (NO-independent signaling) thereby increasing Ca^{2+} (Cyt). Elevated Ca^{2+}(Cyt) induces the expression of abscisic acid–responsive element binding (AREB) protein that binds to the ABA–responsive element (ABRE) motif in the promoter region of ABA-inducible genes. The expression of ABA-responsive genes requires a combination of an ABRE and a coupling element (CE) for a functional promoter. AREB also interacts physically with dehydration responsive element binding (DREB) proteins for the expression of stress responsive genes, leading to stomatal closure under drought conditions.

Under drought condition, H_2O_2 increases cytosolic Ca^{2+} (cyt) either directly by activating Ca^{2+} in channels or indirectly by inducing nitric oxide (NO) synthesis. Increased Ca^{2+} (Cyt) induce the expression of abscisic acid–responsive element binding (AREB) protein. The AREB, a basic domain/leucine zipper transcription factor, binds to the ABA– responsive element (ABRE) motif in the promoter region of ABA inducible genes. According to Fujita *et al.,* (2004) and Nakashima and Yamaguchi-Shinozaki (2013), the expression of ABA-responsive genes requires more than one ABRE or a combination of an ABRE and a coupling element (CE) for a functional promoter. The ABRE mainly mediates downstream gene expression in the ABA-signaling pathway. According to Narusaka *et al.,* (2003), the dehydration responsive element/ C-repeat (DRE/CRT) motif in the promoters of drought-responsive genes, is a binding region for an ABA-independent dehydration responsive element binding (DREB) transcription factor and functions as a CE for ABRE in ABA-dependent gene expression Narusaka *et al.,* (2003) . According to Lee *et al.,* (2010), DREB proteins interact physically with AREB/ABF proteins for the expression of stress responsive gene Fig. (32). Unlike ABA, salicylic acid (SA) mediates ROS production in guard cells via peroxidase-catalyzed reaction not via NADPH

oxidases Mori and Schroeder (2001). Indeed, in the SA-accumulating mutant siz1, the reduced stomatal apertures were inhibited by the application of peroxidase inhibitors such as azide and salicylhydroxamic acid (SHAM; inhibitor of SA dependent ROS production) but not by the NADPH oxidase inhibitor i.e. diphenyliodonium chloride (DPI) (inhibitor of ABA-dependent ROS production) Miura *et al.,* (2012). Pre-treatment with CAT and SOD, inhibited the SA induced stomatal closure thereby suggesting that extracellular ROS are involve in stomatal movement Khokon *et al.,* (2011).

Furthermore, SHAM (a peroxidase inhibitor) eliminates SA-induced stomatal closure while neither atrbohD and atrbohF mutation nor DPI (an inhibitor of NADPH oxidase) impairs SA-induced stomatal closure Khokon *et al.,* (2011). SA considerably increased ROS accumulation in guard cell, but those ROS were holdback by exogenous SHAM, SOD, and CAT. According to Khokon *et al.,* (2011), SA was failed to stimulate Ca^{2+} (cyt) oscillations while SA suppressed K^+ in channel activity, in guard cells. These findings point out that SA induces stomatal closure along with extracellular ROS generation mediated by SHAM-sensitive peroxidase, intracellular ROS accumulation and inactivation of K^+ in channels Khokon *et al.,* (2011). In contrary to this, Kalachova *et al.,* (2013) reported that SA-induced stomatal closure is impaired by DPI [an NADPH oxidases (NOX) inhibitor that inhibits ROS production] treatment and NOX deficient plants showed inhibited stomatal reaction even after exposure to exogenous SA Kalachova *et al.,* (2013).

Thus, it can be concluded that NOX plays a critical role in stomatal closure in response to SA also. ROS are also generated by G protein-coupled receptor (GPCR), Arabidopsis αsubunit of the trimeric G protein (GPA1), and salicylic acid signaling network complexes i.e. phospholipase C (PLC) and phosphatidic acid (PA) either directly or by activating NOX, which leads to increased cytosolic Ca^{2+}(cyt). Further, based on the observation, a fundamental link between ABA and SA signaling has been suggested, as in ABA deficient aba2-1 mutant no longer stomata were closed in response to exogenously applied SA; while SA-deficient nahG and sid2 mutant responded normally to ABA in guard cells Zeng and He (2010), Kalachova *et al.,* (2013) . These findings, therefore, imply that SA signaling acts in up streaming of ABA signaling and signifies that interaction between SA and ROS can differ under different concentrations and conditions. Another phytohormone methyl jasmonate (MeJA) has also been known to elicit the ROS generation in guard cells Leshem and Levine (2013). MeJA-induced stomatal closure was suppressed by exogenous application of DPI. In the same study, the NADPH oxidase double mutant atrbohD/F, MeJA could not induced stomatal closing. These observations suggest that major sources of ROS in MeJA induced signaling in guard cell is NADPH oxidases AtrbohD/F Suhita *et al.,* (2004) . In the rcn1 mutant (mutation in gene encoding a regulatory subunit of protein phosphatase type 2A (PP2A)) of A. thaliana, MeJA failed to elicit the ROS and NO generation Saito *et al.,* (2008). These findings suggest that in MeJA induced signaling of guard cell; RCN1-regulates PP2As function by up streaming of ROS and NO generation.

When addressing oxidative stress signaling, the role played by transcription factors cannot be neglected. Any stimulus that increases ROS and/or decreases antioxidant activity of the cell disturbs the redox balance and thus induces oxidative stress. Several redox controlled transcription factors have been identified. Thiol groups are probably important in redox signal transduction, including ROS sensing by receptor kinases that mediates stomatal closure in response to H_2O_2 Desikan *et al.,* (2005). For instances, a bacterial H_2O_2 sensor i.e. OxyR was firstly identified transcription factor in Salmonella species and *Escherichia coli* Stone (2004), D'Autreaux and Toledano (2007) . Oxy R, activated by H_2O_2, is a homodimer formed by an intermolecular disulphide bridge which brings out some significant alterations in the structure of protein Stone (2004), while deactivated by enzymatic reduction with glutaredoxin 1 (Grx1); the gene encoding Grx1 regulated by OxyR. Among the transcriptional factors, heat shock transcription factors (HSFs) are potential ROS sensors. HSFs are necessary not only for defence/protection against high-temperature stress, but also involved in the modulation of different abiotic stress responses Akerfelt *et al.,* (2007), Anckar *et al.,* (2011) . HSFs play a central role in the early sensing of H_2O_2 and participate in signaling crosstalk with several key components of H_2O_2 signaling Pucciariello *et al.,* (2012). According to Miller and Mittler (2006), HSFs play the role of molecular peroxide sensor and cause the conformational changes and multimeric formation thereby altering the H_2O_2 concentrations during stress which concomitantly leads to transcriptional activation of their target genes. The member of other transcription factor families i.e. GRAS, Myb, RAV, WRKY, and Zat are also activated by ROS Tripathy and Oelmuller, (2012). During abiotic stresses and in response to wound-induced signaling, the expression of a zinc finger protein Zat12 (Zat12 is a vital part

of the oxidative stress response signal transduction network of *Arabidopsis* is activated at the transcriptional level as determined by fusion between the reporter gene luciferase and the Zat12 promoter Davletova *et al.,* (2005). The nonexpressor of pathogenesis-related genes 1 (NPR1) transcription factor, is responsible for the modulation in the alterations of gene expression during systemic acquired resistance in plants. NPR1 exists as an oligomer in non-activation state, which is maintained by intermolecular disulphide bonds; while on activation, NPR1 get reduced to a monomeric form which after that accumulates in the nucleus and alters the gene expression Mou *et al.,* (2003).

8.2. ATP Synthesis and Energy Flow

Mitochondria provide majority of the energy required for proper cellular functioning; hence, any damage to it results in decreased or inefficient energy production and consequently hindrance in ATP-dependent cellular mechanisms Maurer and Meyed 2016).Fig. (33), (34).

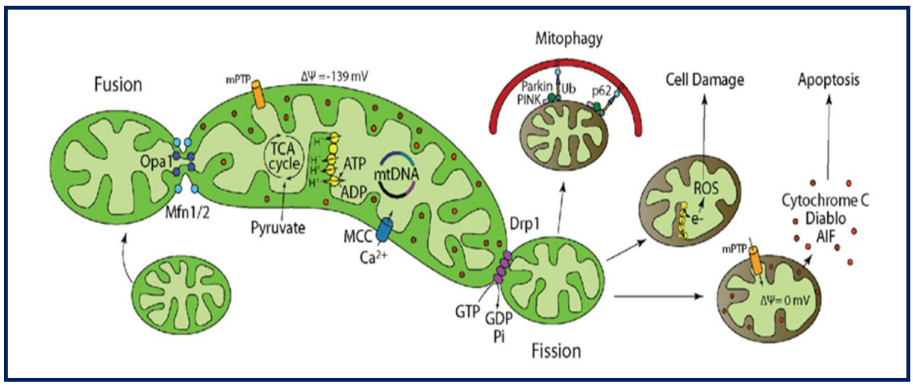

Fig. 33: Mitochondrial dynamics and function regulate cellular energy homeostasis, cell survival, growth, and death. Inside of a cell, mitochondria are in a dynamic flux, continuously undergoing fusion and fission to meet cellular energy needs. (1) Fusion is regulated by Optic Atrophy 1 (Opa1) and Mitofusin1/2 (Mfn1/2) and allows for functional complementation and repair of damaged mitochondria. (2) Pyruvate from glycolysis is transported into the mitochondria where pyruvate dehydrogenase catalyzes the decarboxylation of Pyruvate to form Acetyl CoA. Acetyl CoA then enters the TCA cycle. (3) Electromotive force generated by the electron transport chain allows ATP synthesis by the F1-Fo ATP synthase. (4) Mitochondria buffer excess intracellular calcium. When calcium buffering capacity is compromised as a result of mitochondrial damage/depolarization, calcium accumulates in the cytosol and activates degradative enzymes such as calpain and phospholipases that break down cellular proteins and membrane leading to death. (5) Fission is regulated by dynamin-related protein 1 (Drp1) and allows for mitochondria that cannot be repaired to be isolated followed by degradation through mitophagy. Fission is also important for subcellular distribution and transportation of mitochondria based on energy needs in certain areas of the cell. (6) Electrons leaked from the electron transport chain interact with molecular oxygen to generate reactive oxygen species (ROS) that not only damage mitochondrial membrane, mitochondrial DNA (mtDNA), and proteins, but also their cellular counter parts. Neurons have limited defense against oxidative damage and are highly vulnerable to ROS. (7) Mitochondria play a prominent role in apoptotic cell death. Damaged/depolarized mitochondria release cytochrome c and apoptosis inducing factor (AIF) that trigger cell death by activating caspases After Fischer *et al.,* (2016)

Fischer *et al.,* (2016) reported that the UPS has a profound role in many aspects of mitochondrial biology. We have highlighted how mitochondrial-associated DUBs plausibly are novel players in pathways that inevitably lead to proteasomal degradation. Deubiquitinases also have the potential to drive the kinetics of other ubiquitin-mediated pathways such as mitophagy. It is well established that mitophagy is initiated by the accumulation of PINK1 on the OMM. Here, we have discussed how PARL affects PINK1 localization under normal versus stress conditions and, hence, how PARL might add in another layer of regulation to refine the process of mitophagy. The UPS and mitophagy are two of multiple quality control mechanisms that maintain functional mitochondria. These organelles may have adopted diverse reparative processes so that no one mechanism is overwhelmed at any given time. It is

likely that different factors, such as ATP availability, ROS levels, and mitochondrial membrane potential, stimulate certain pathways. Both the UPS and mitophagy require ATP; hence, oxidative phosphorylation has an influence on mitochondrial quality control systems. Conversely, components of mitophagy also influence OXPHOS. Mutations in Parkin as well as defects in PINK1 adversely affect mitochondrial respiration. Furthermore, mutations in ataxin-3 affect complex II activity Fig. (33).

Considering the high interconnectivity of different mitochondrial functions, one of the downstream effects of quality control failure is intrinsic apoptosis. The proper functioning of the mitochondrial UPS is required to maintain sufficient levels of antiapoptotic proteins, such as Mcl1. While, mitophagy is essential for preventing an accumulation of damaged mitochondria in the cell that could elicit cell death. To fully understand the larger implications of mitochondrial quality control systems and mitochondrial dysfunction, we must consider the contributing factors such as energy metabolism and the downstream consequences such as apoptosis Fig. (33). Hence, further studies are required to investigate mitochondrial UPS and mitophagy pathways and to understand how perturbations of these systems relate to overall cellular metabolic states. Because proteolysis is becoming a central theme in regulating all of these integrated pathways and, because proteases are ideal drug targets, there will be intense interest in both academic laboratories and pharmaceutical companies to understand the precise molecular pathways of MAD and mitophagy. New discoveries in this mitochondrial quality control Systems and their roles in overall cell integrity will continue to enlighten us on the pathogenesis of neurodegenerative diseases like PD.

They also stated that mitochondria are at the crossroad between cellular health, survival, and death. Mitochondria not only provide cellular energy through ATP synthesis, but also play an important role in intracellular calcium buffering, reactive oxygen species (ROS) production, and apoptosis. A growing body of literature from both clinical and experimental brain injury research has shown that structural and functional damage of mitochondria is an early event after traumatic brain injury (TBI) that contributes to cell death and poor cognitive outcome Vink *et al.,* (1990); Okonkwo and Povlishock, (1999); Sullivan *et al.,* (1999); Lifshitz *et al.,* (2003), (2004); Singh *et al.,* (2006); Cheng *et al.,* (2012); Caravelli *et al.,* (2015). Decreased respiration and reduced ATP production in cortical and hippocampal mitochondria occurs within 24 h post-injury and can last up to 14 days in experimental models of TBI Xiong *et al.,* (1997); Lifshitz *et al.,* (2003); Singh *et al.,* (2006); Gilmer *et al.,* (2009). Moreover, mitochondrial damage can result in the release of pro-apoptotic factors, such as cytochrome C, that activate cell death pathways and initiate apoptosis Raghupathi *et al.,* (2000); Brustovetsky *et al.,* (2002). As neurons have high metabolic needs and do not store excess energy, continuous energy production and metabolic maintenance by functional mitochondria is critical for survival, supporting the premise that improving mitochondrial function can offer neuroprotection and improve cognition following TBI Cheng *et al.,* (2012); Caravelli *et al.,* (2015). Mitochondria are dynamic organelles that continuously undergo fusion and fission to form a highly interconnected network throughout the cell Bereiter-Hahn and Vöth, (1994); Chan, (2006); van der Bliek *et al.,* (2013).

These balanced processes alter mitochondrial morphology and allow mitochondria to efficiently respond to cellular energy needs Bereiter-Hahn and Vöth, (1994); Chan, (2006); Westermann, (2012); van der Bliek *et al.,* (2013). Fusion allows for an increase in cristae density and maximization of ATP production during high metabolic activity and stress Westermann, (2012); Youle and van der Bliek, (2012). In contrast, fission allows for proliferation and transportation of mitochondria to areas with energy demands, in addition to segregation of damaged mitochondria from the network for subsequent degradation through mitophagy Youle and van der Bliek, (2012); Otera *et al.,* (2013). An imbalance between fusion and fission, particularly an excess of fission, can be detrimental for energy homeostasis and has been implicated in neurodegenerative diseases Detmer and Chan, (2007); Knott and Bossy-Wetzel, (2008); Knott *et al.,* (2008); Archer, (2013); Burté *et al.,* (2015). More specifically, excessive fission can lead to reduced mitochondrial respiration and ATP production, increased ROS generation, and release of apoptogenic factors, changes similar to those seen after TBI Fig.(34) ; Rintoul *et al.,* (2003); Chen *et al.,* (2005); Cribbs and Strack, (2007); Detmer and Chan, (2007); Yu *et al.,* (2008a); Chen and Chan, (2009); Costa *et al.,* (2010); Jahani-Asl *et al.,* (2011); Jheng *et al.,* (2012).

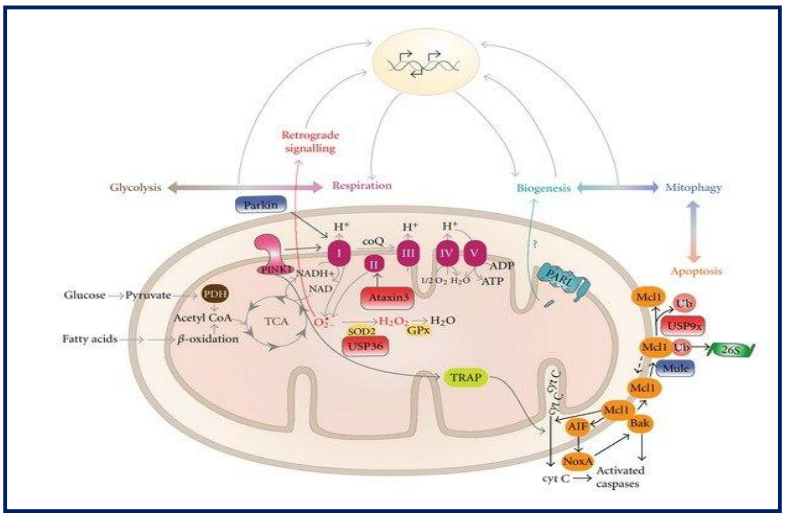

Fig. 34: Interdependence of mitochondrial functions. Mitochondria generate ATP energy for the cell with the help of the electron transport chain. ATP fuels many cellular processes including protein degradation by the 26S proteasome. Hence, the process of oxidative phosphorylation (OXPHOS) influences the function of mitochondrial quality control systems. In the reverse direction, components of the quality control pathways can influence OXPHOS. Parkin mutants and defects in PINK1 have been shown to reduce mitochondrial respiration; PINK1 defects impair complex I functionality. In addition, mammalian studies with ataxin-3 mutants showed reduced complex II activity. Mitochondrial dysfunction can trigger apoptosis. Failures within the quality control system, coupled with an increase in ROS, can lead to the release of proapoptotic proteins. For example, if sufficient amounts of Mcl1 are not maintained due to unrestrained proteasomal degradation, Bak can facilitate the release of AIF/cyt C and induce apoptosis. Hence, it is important for the quality control mechanisms to function properly in order to prevent unsolicited downstream effects. Overall, the mitochondrial network has to maintain a refined balance between all of these processes and direct effective metabolic outputs depending on the environmental and/or developmental context. After Fischer *et al.,* (2016)

Dynamin-related protein 1 (Drp1) is a key regulator of mitochondrial fission, through its interactions with the mitochondrial outer membrane (MOM; van der Bliek *et al.,* (2013). Prior to a fission event, Drp1 translocates to the MOM where it self-assembles and forms an oligomeric structure around the mitochondrion. Hydrolysis of Drp1-bound GTP then drives the subsequent mitochondrial membrane division. Mitochondrial division inhibitor-1 (Mdivi1) is an allosteric inhibitor of Drp1 that inhibits its oligomeric assembly thereby reducing its GTP binding affinity CassidyStone *et al.,* (2008). Mdivi-1 has been shown to reduce cell death by attenuating mitochondrial fission in yeast, and in animals models Cassidy-Stone *et al.,* (2008); Jahani-Asl *et al.,* (2011); Grohm *et al.,* (2012); Rappold *et al.,* (2014); Zhao *et al.,* (2014). Recently, a study has reported that Mdivi-1 reduces cortical cell loss and improves spatial memory after TBI in mice Wu *et al.,* (2016). However, it is unknown if TBI alters Drp1 translocation to the MOM and mitochondrial dynamics.

Generation of intracellular ROS is postulated to be an important mitochondrial mechanism of AgNP toxicity and has been documented in cell too. Multiple mechanisms exist for AgNP-mediated ROS generation, including NP surface chemistry, depletion of antioxidant molecules via binding of dissolved ions with their thiol groups, altered production of ROS, and inhibition in the electron transport chain Asha Rani *et al.,* (2009). Fig. (35). Tripathi *et al.,* (2017b) documented that in most cell types and under most circumstances, mitochondria are the major source of ROS production and major target for oxidative damage, resulting in the mitochondrial specifc dysfunction such as ATP production.

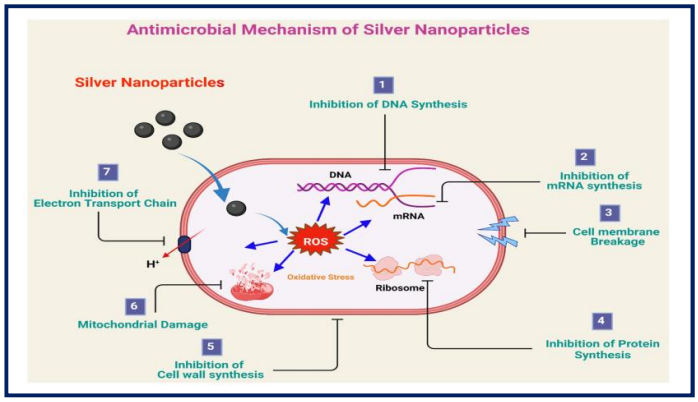

Fig. 35: Antimicrobial mechanism of silver nanoparticles: (1) inhibition of DNA synthesis, (2) inhibition of mRNA synthesis, (3) cell membrane destruction and the leakage of the cell constituents, (4) inhibition of protein synthesis, (5) inhibition of cell-wall synthesis, (6) mitochondrial damage, and (7) inhibition of electron transport chain. Figure 1. Antimicrobial mechanism of silver nanoparticles: (1) inhibition of DNA synthesis, (2) inhibition of mRNA synthesis, (3) cell membrane destruction and the leakage of the cell constituents, (4) inhibition of protein synthesis, (5) inhibition of cell-wall synthesis, (6) mitochondrial damage, and (7) inhibition of electron transport chain. After Jain *et al.,* (2021).

8.3. Nutrient and Water

Uptake in plants, uptake of nutrients is the principal process involving absorption of essential elements from the environment. Regulation of nutrient uptake has mostly been considered in relation to the factors that directly affect the rate of membrane transport. Nutrient uptake and transport through the cell membrane is an important task of all the living organisms. However, AgNPs signifcantly affect the membrane fluidity and permeability and consequently influence the uptake of water and nutrients. Decline in water content was observed, in dose-dependent manner, in seedlings of Raphanus sativus after AgNP treatment Zuverza-Mena *et al.,* (2016). They also observed the reductions in many plant nutrients like Ca, Mg, boron (B), copper (Cu), manganese (Mn), and Zn by exposure of AgNP, which ultimately affect the plants growth and development. Tips of primary roots are major sites of AgNP accumulation. However, plants mitigate this toxic effect of AgNP by forming lateral roots that compensate for the loss of primary root growth, continuing to absorb the water and nutrients that sustain an overall growth of plants Pokhrel and Dubey (2013).

9. Silver Nanoparticle as Ameliorative Molecule against Other Toxicity

The combined effects of AgNPs with other treatments (heavy metal, salt stress, pathogens) were observed in various studies, which showed diverse impacts on different plant species Berahmand *et al.,* (2012). Treatment of AgNP in combination with magnetic field improved growth and yield of Zea mays Berahmand *et al.,* (2012).

Maulucci *et al.,* (2012), seven treatments based on a randomized complete block design in four replications were tested. The treatments were as follows: magnetic field and silver nanoparticles + Kemira commercial fertilizer (T1), magnetic field and silver nanoparticles + Humax commercial fertilizer (T2), magnetic field and silver nanoparticles (T3), Kemira fertilizer (T4), Librel commercial fertilizer (T5), Humax fertilizer (T6), and a control (T7). In each plot, a distance of 75 cm was set between the rows, and the final plant density was 11.1 plants per square meters. The maize variety was SC 704. A plot size of 3.5×6 m was used. For all treatments, nitrogen fertilizer (as urea) on the basis of 250 and 250 kg ha^{-1} phosphorus fertilizer (as phosphate ammonium), 250 and 150 kg ha^{-1} and potassium fertilizer (as potassium sulfate), 120 and 50 kg ha^{-1} , were applied in 2008 Iran. Agronomic traits of maize such as fodder fresh yield, fodder dry yield, plant dry matter, plant height, and plant components (leaf, stem, and ear) were measured at harvest time. 2009, respectively.

Pesticides, herbicides, and fungicides were not used for controlling pests, diseases, and weeds during the growing seasons. Weeds were managed by hand weeding throughout the growing season.

Ingredients of Humax fertilizer consisted of 12 % humic acid, 3 % folic acid, and 3 % K_2O. Components of Kemira and Librel fertilizers were 20 % K_2O, 20 %N, and 20 % P_2O_5 and micronutrients (Fe, Zn, Mn, Cu, Mo, B, and Mg). Humax and Kemira fertilizers were applied as Fertigation and Librel fertilizer by foliar application according to factory recommendations. After seed emergence, magnetic field treatment was done by employing magnet pieces with dimensions of 3× 1 cm and strength of 10 mT, located adjacent to or near each plant on the soil's surface. At the same time, 40 gha^{-1} of colloidal nanosilver was used in the irrigation water for the silver nanoparticle treatment. The average size of silver nanoparticles was around 20 nm, determined by transition electron microscope (TEM) in the Central Laboratory of Ferdowsi University of Mashhad. They observed that applications of a combination of silver nanoparticles and magnetic field led to improved quantitative yields of fodder maize, especially in 2008. Similar effects were demonstrated on the studied traits in 2009. Nevertheless, results were more significant in 2008 than 2009. It is probable that there were more suitable soil conditions for crop growth in 2009 than in 2008 and that this caused the lower response from plants to the treatments tested in this experiment. The treatment combining silver nanoparticles and magnetic field (T3) most effectively improved the quality of fodder maize for animal feed compared to other treatments.

Moreover, Belava *et al.,* (2017) observed the oxidative stress condition and enhancements in lipid peroxidation after alone treatments of AgNP and infectious agents (pathogens) in Triticum aestivum. However, the combined treatment of AgNP and plant-pathogenic fungi showed the reverse impact and eliminated this organism, due to the fungicidal activity of AgNP Jo *et al.,* (2009). Traces of essential heavy metals such as Cu, molybdenum (Mo), and Zn can be necessary for plant metabolism, but their excess can harm plant growth and development. However, non-essential heavy metals are toxic for plant metabolism and have damaging effects, even if available in trace amounts, on enzyme activity, photosynthetic properties, cell membrane permeability, and plant growth Emamverdian and Ding (2017).

Yadu *et al.,* (2018) reported that ameliorative influences of AgNP on the growing radicles of Cajanus Cajan against fluoride toxicity. Exogenous application of AgNP under fluoride stress not only down regulated the expression of NADPH oxidase gene and lipoxygenase activity but also promoted the membrane stability, percent germination, and growth by reducing the levels of ROS. Moreover, AgNP unveiled enhancement in F- stress tolerance through up-regulation of stress responsive gene like pyrroline-5-carboxylate synthetase and increased the synthesis of proline in Cajanus cajan radicles. Additionally, enhanced levels of defensive components such as glutathione, glyoxalase I, glyoxalase II, and lower malondialdehyde also approved the ameliorative abilities of AgNP to F- stress. Likewise, toxic impacts of arsenic (As), cadmium (Cd), and Cu were compared with their combinations made with citrate-coated AgNPs (c-AgNPs). The surface of c-AgNP has negative charge, which interacts with the surface of heavy metals and affects metal toxicity in aquatic environment. The acute toxicities of As and Cu were not affected by the addition of c-AgNPs, while signifcantly decline in bioaccumulation was observed. In contrast to this, the presence of c-AgNPs increased both the acute toxicity and bioaccumulation of Cd. The diverse toxicity and bioaccumulation pattern can be attributed due to the altered interactions between the AgNP surface and the heavy metals. The As and c-AgNPs compete due to the negative charge on their surfaces, while Cu adheres to the surface of c-AgNP, consequently decreasing the toxicity and bioavailability of As and Cu, respectively Kim *et al.,* (2016)

10. Effect of nanomaterial (types and time of exposure) on changes in protein expression

Nanomaterial phytotoxicity has attracted attention in recent years. The mechanisms involved in changes of plant protein expression due to the exposure to nanoparticles treatments are still unknown, it is necessary to develop a more standardized approach in order to understand the interaction between plant and nanomaterial. Using Proteomics techniques, for detection changes in protein expression profiles for both quantitative and qualitative, are powerful tool for the identification of proteins related to specific developmental and/or environmental signal Gygi and Aebersold (2000). Proteomic studies can improve the knowledge of interactions between plants and nanomaterial, that reflecting the effects on gene expression. Several researchers Vannini *et al.,* (2013), (2014), Peharec *et al.,* (2018), Mirzajani *et al.,* (2014) , Mustafa *et al.,* (2015) reported that studying plant responses to AgNP-induced stress has been employed in only a few studies. On the current literature since results of these studies offer new

insight into plant response to AgNP exposure and provide important information to support the sustainable use of AgNPs.

Through roots, stomata, or epidermal absorption in leaves, NPs enter the plant because of their quite small size. Through the apoplastic or symplastic pathway, NPs enter the cells and reach various plant systems in the case of roots. NPs enter the cell membrane through the cell wall in the root's epidermis, where they are symplastically transported to the vascular system. Pore size is a factor in movement through the cell membrane or cell wall Shukla *et al.,* (2016), Ali (2021). In addition to travelling through the symplastic pathways, NPs also travel via the apoplastic pathway to reach the vascular system. After they enter, NPs are moved to the plant's leaves, where they come in contact with chloroplast, which results in the disruption of the plant's physiology Kang *et al.,* (2023). A brief explanation of how NPs make their way to a plant's system is provided in the schematic illustration in Fig. (36).

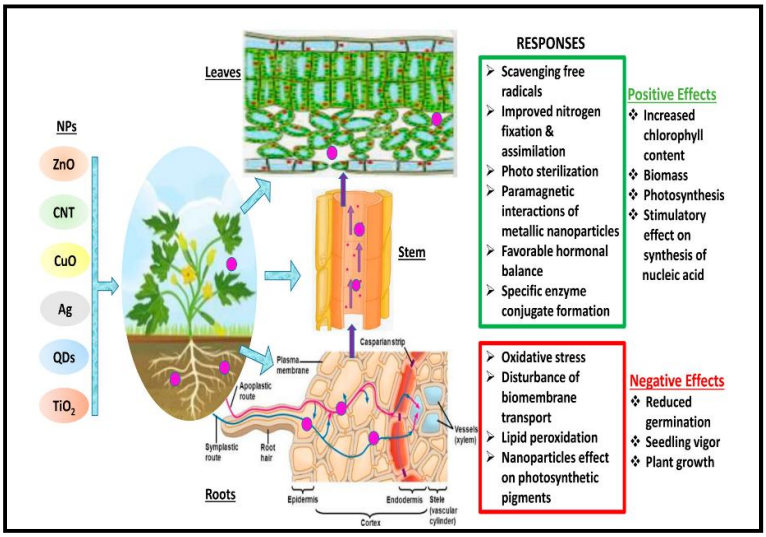

Fig. 36: Schematic diagram of plant—NPs interactions and various responses. (Red color indicates the negative influences of NPs interaction in plants, whereas green color shows the positive interactions of NPs in plant cells). After Munir *et al.,* (2023).

Leaves contain two entry points: one is via absorption through the leaf's epidermis and the other through the stomata. In a study, it was demonstrated through confocal microscopy that NPs enter Vicia faba at a specific size through the stomata; NPs of 1.1 µm did not penetrate the cell system; those of 43 nm did. Cerium (37 nm) enter the plant system but are not translocated to the stem, as observed in leaves of Zea mays using electronic and confocal microscopy and mass spectrometry Eichert *et al.,* (2008) ; however, this study was unable to determine whether the stomata or the leaf epidermis were the entry points Birbaum *et al.,* (2010) .

Similarly, in another study using X-ray and electron fluorescence microscopy on *Arabidopsis* seedlings, NPs entered the epidermis through stomata and were absorbed by endocytic vessels to reach the palisade layer Kurepa *et al.,* (2010), Wang *et al.,* (2010) . Several studies have been carried out to investigate entry through the leaf's epidermis in addition to those focused on stomatal entry. The work carried out by some researchers, using nonionic colloidal solutions of iron, zinc, and manganese, demonstrated that these are translocated after being absorbed by the leaf epidermis Taran *et al.,* (2014). Another study found that both bulk salt and Ag NPs (both with 47.9 nm hydrodynamic diameter) entered Lactuga via absorption through the cuticle and stomata before being transported to the vascular system. The study also unveiled that Ag^{+} is interconverted into Ag NPs by binding with thiol groups Larue *et al.,* (2014).

Maize, rapeseed, spinach, and desert plants have been the subject of numerous studies Taran *et al.,* (2014), Zheng *et al.,* (2005), Racuciu *et al.,* (2009), De La Rosa *et al.,* (2011) and it has been demonstrated that NPs make their way to the root system through the epidermis, then translocate to the

stems, and leaves Rico *et al.,* (2011). In another study, the entry of iron oxide (Fe_2O_3) NPs through the root epidermis was found in pumpkin plants grown in an aqueous medium, and further translocation to shoots and leaves was observed as well Zhu *et al.,* (2008). In another study, 2.8 nm sized Ti nanoconjugates were found to be penetrated into root cells and transported to nucleus and vacuoles in *Arabidopsis thaliana* Kurepa *et al.,* (2010). Transmission electron microscopy revealed the adherence and accumulation of Ti NPs in the cell wall of roots, as well as further translocation of particles in the cortex and then to the vacuoles Du *et al.,* (2011) . In addition, a number of experiments using confocal microscopy, X-ray fluorescence, and coupled plasma optical emission spectrometry reported that NPs entered the plant via the roots before being transferred to the shoots via the apoplastic pathway Zhao *et al.,* (2012), Zhao *et al.,* (2014) Additionally, analysis on soil systems averred that organic substances in the soil influence NP mobility.

Since nanotechnology has been recognized as the most cutting-edge, rapidly developing, and laborsaving technology by the scientific community as of late, it now has applications in almost every field of science. The toxicity caused by the constant deposition of NPs in the environment is not ignorable, especially in terms of plant performance. NPs interaction at genomic level is shown in Fig. (37) A bulk of the literature demonstrates the morphological and physiological phytotoxic effects of NPs, but very little demonstrates the gene-level toxicity of NPs. Researchers reported that CuO NPs were toxic to some agricultural crops like Loliumrigidum, Lolium perenne and Raphanus sativus, Lolium rigidum, Lolium perenne, and Raphanus sativus, and after prolonged NP exposure, DNA was destroyed. The deposition of compounds that have been altered by oxidation led to the formation of mutagenic DNA lesions, which in turn caused rapid disruptions in plant growth Atha *et al.,* (2012) . Similarly, ZnO NP toxicity in wheat seedlings was examined and it was discovered that nitric oxide (NO) mitigates this toxicity in wheat effectively Tripathi *et al.,* (2017). Additionally, figuring out the NPs' genotoxic endpoints is a concern because they have been linked to metal's genotoxic effects in plants Rodriguez *et al.,* (2011) , but any generalizations regarding NP-induced phyto genotoxicity must be handled with care.

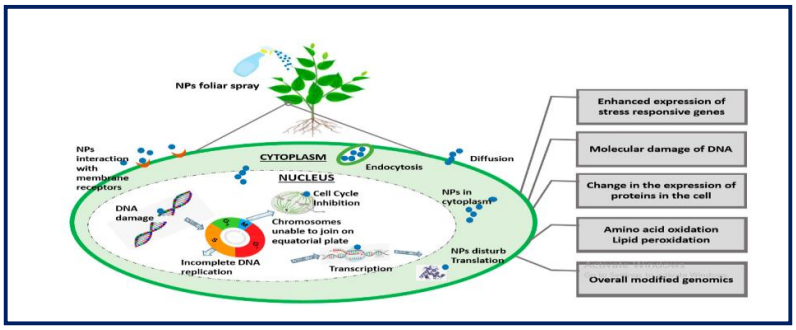

Fig. 37: A brief illustration of genomic insight into plant—NPs interaction. After Munir *et al.,* (2023)

The obtained results is difficult to draw unambiguous conclusions since in different studies different sizes of nanoparticles were applied and AgNPs were stabilized with different coatings or were uncoated. Mirzajani *et al.,* (2014) reported that exposure of rice seedlings to 18.34 nm uncoated AgNPs; 15nm AgNPs without coating were also applied in treatments of soybean seedlings Mustafa *et al.,* (2015). Proteomic studies of exposure of rocket and wheat seedlings, 10 nm AgNP-PVP were used by Vannini *et al.,* (2013), (2014), however AgNP-citrate was examined in tobacco seedlings 50 nm, Peharec *et al.,* (2018) and soybean plants 60 nm, Galazzi *et al.,* (2019). Moreover, the exposure times also differed among published studies and extended from short exposures of two Mustafa *et al.,* (2015)., three Lindgren (2014) or 5 days Vannini *et al.,* (2013), (2014) to much longer treatments which lasted for 14 Galazzi *et al.,* (2019), 20, Mirzajani *et al.,* (2014) and 30 days Peharec etal (2018) Fig. (38).
Exposure media used for AgNP-treatments included soaked filter paper Vannini *et al.,* (2013), (2014), silica sand Mustafa *et al.,* (2015), liquid Mirzajani *et al.,* (2014), Lindgren (2014) or solid nutrient medium Peharec *et al.,* (2018) and deionized water Galazzi *et al.,* (2019).

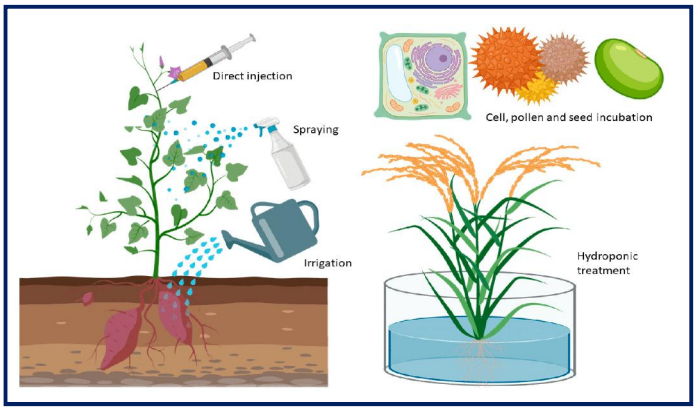

Fig. 38: Different types of nanoparticles (NP)/plant exposure methodologies. After Paramo *et al.,* (2020).

The toxicological effects of the NPs are determined not only by the physicochemical characteristics, but also by the experimental design synthesis, the exposure time over the plant, the development phase in which the NP will come into contact with the plant, as well as the means of introduction and interaction of the NPs. There are different methodologies to expose the plant to the NPs Fig. (38) , such as the direct injection of NPs into plant tissue Corredor *et al.,* (2009) , NPs spraying into leaves or any other part of the plant Tarafdar *et al.,* (2012) , contaminating the soil with NPs or irrigating plants with NP suspensions Zhu *et al.,* (2008) , and infecting cellular pollen or seeds Poborilova etal (2013) , Yin *et al.,* (2012)

Fully developed seedlings prolonged exposure of the seedlings to silver treatments , observed that changes in the proteomes always reflect the adjustment of plant metabolism to AgNP-induced stress. Contrary, in the following studies, where proteome changes were analysed after a few days of exposure, differences in protein expression might be a result of instant up-/down-regulation in response to AgNPs. After five day of exposure to rocket seedlings by AgNP-PVP, only the proteome of root tissue was analysed and 22 AgNP-responsive proteins were found, among which 15 proteins exhibited enhanced expression Vannini *et al.,* (2013). Similar treatment were applied to wheat seedlings which resulted with 27 responsive proteins in roots and 12 in shoots, majority of which was up-regulated; interestingly, no common proteins in roots and shoots were found Vannini *et al.,* (2014). Mustafa *et al.,* (2015) reported that in the differential analysis of soybean seedlings exposed to uncoated AgNPs, the abundances of 107 root proteins were significantly changed, while in cotyledons only 9 proteins were found to be responsive; majority of the proteins were found to be down-regulated.

Glyoxalase II 3 protein was only found to be common for roots and cotyledons, although its response was opposite; in the root tissue, glyoxalase II 3 expression was down regulated, while in cotyledons, it revealed enhanced expression. In both roots and shoots of adult tobacco plants, only several common proteins (osmotin, basic beta-1,3-glucanase, CBP20, Fe-SOD, glyceraldehyde- 3-phosphate dehydrogenase (GAPDH), triose phosphate isomerase (TPI) and malate dehydrogenase (MDH)) were found to be regulated by AgNPs. This phenomenon due high accumulation of silver in roots than in leaves, after both types of treatments.

Additionally, studies in which coated AgNPs (PVP Vannini *et al.,* (2013), (2014), PEG, Lindgren (2014), and citrate, Peharec *et al.,* (2018) were applied, resulted with mostly up-regulated responsive proteins, while in two studies performed with uncoated AgNPs Mirzajani *et al.,* (2014), Mustafa *et al.,* (2015) majority of the proteins exhibited decreased expression, which related with higher stability of coated AgNPs, that are less prone to release Ag^{+} ions compared to uncoated ones.

Different types of coating agents were used for AgNP stabilization. The PubMed search performed for this review resulted in 16 different coatings used in the assessment of AgNP toxic effects in both plants and freshwater green algae. AgNP stabilization is usually obtained by either steric stabilization, which arises because of polymer adsorption onto the surface of particles Koczkur *et al.,* (2015), or electrostatic stabilization, which includes surface charge development, usually by physical adsorption of charged species onto the surface Yu *et al.,* (2012). Among nonionic polymer coatings, the

most frequently used one is PVP, which has been applied in numerous investigations performed on plants Zhang *et al.,* (2019),Peharec *et al.,* (2021) and algae Wang *et al.,* (2016), Navarro *et al.,* (2015),, Wang *et al.,* (2015) . Besides PVP, polyethylene glycol (PEG) and poly vinyl alcohol (PVA) have also been frequently used for AgNP stabilization in both plant Wang *et al.,* (2013), Lalau *et al.,* (2020) and algal research Matorin *et al.,* (2013), Navarro *et al.,* (2015), Pham (2019), Lindgren *et al.,* (2014), while GA, a natural polymer consisting of polysaccharides and glycoproteins, has mostly been utilized in plant studies Yin *et al.,* (2011), Jiang *et al.,* (2017), Jiang *et al.,* (2012), Kong *et al.,* (2014).

Considering the electrostatic stabilization of AgNPs, citrate is the most commonly applied coating that provides a negative charge, and it has been employed in many toxicology studies performed on both plants Cvjetko *et al.,* (2018) Biba *et al.,* (2020), Peharec *et al.,* (2021), Biba *et al.,* (2021), , Abdel-Aziz and Rizwan(2019) and algae Navarro *et al.,* (2015), Romero *et al.,* (2020), Zhang *et al.,* (2029), Kalman *et al.,* (2015), Angel *et al.,* (2013), Yue *et al.,* (2017), Zhou *et al.,* (2016), Li *et al.,* (2013) . On the other hand, positively charged AgNPs have been scarcely used in plant studies and were usually obtained by application of cationic surfactant CTAB Biba *et al.,* (2020), Peharec *et al.,* (2021), Cvjetko *et al.,* (2017) , although didecyldimethylammonium bromide (DDAB) Barabanov *et al.,* (2018) or poly hexa methylene biguanide (PHMB) Gusev *et al.,* (2016) have also been employed. Cationic polymer polyethyleneimine (PEI) was applied as AgNP coating in the study on freshwater algae C. vulgaris Zhang *et al.,* (2020). In this, we attempt to give an overview on how employment of different stabilizing coatings can modulate AgNP-induced phytotoxicity with respect to growth, physiology, and gene and protein expression in terrestrial and aquatic plants and freshwater algae. Moreover, this is, to our knowledge, the first publication to summarize all aspects of AgNPs toxicity on freshwater algae.

A thorough physicochemical characterization of AgNPs used for toxicological investigations is needed both prior and during the experiment, considering that different exposure conditions may affect their size, shape, and surface electric charge Zhao *et al.,* (2012), Argentiere *et al.,* (2016) and, consequently, alter their uptake, toxic kinetics, toxic dynamics, and biological fate Liu *et al.,* (2011), Pem *et al.,* (2021). Biological media have a high chemical complexity, which is determined by pH, ionic strength, and various concentrations of dissolved organic and inorganic matter. Therefore, it is impossible to correctly predict the form (particulate or ionic) and dose of silver the system is exposed to MacCuspie (2011) due to the interactions of AgNPs and the medium that can lead to both agglomeration/aggregation of nanoparticles and their dissolution Akter *et al.,* (2018), Tejamaya *et al.,* (2012) . On top of that, chemical or photo-induced reduction of Ag^{+} ions released from the AgNP surface can lead to formation of secondary particles with different characteristics compared to the original ones Argentiere *et al.,* (2016), Azodi *et al.,* (2016), Reidy *et al.,* (2013).

Therefore, understanding AgNP dynamics in exposure medium used for plant and algae treatment plays a key role in interpretation of those toxicological studies. Colloidal stability of AgNPs in different media used for plant and algal nanotoxicological studies is greatly determined by the composition of the medium itself and the exposure period of the treatment, Tkalec *et al.,* (2019), Biba *et al.,* (2021) . Moreover, intrinsic properties of AgNPs (size, shape, and surface charge) also direct their behavior in the environment Sharma *et al.,* (2014). Generally, rate of dissolution is higher for smaller uncoated AgNPs in media rich in molecules that tend to complex released Ag^{+} ions Muraleetharan *et al.,* (2019). Plant experiments conducted with uncoated AgNPs revealed significantly higher agglomeration and dissolution rates of AgNPs in tested liquid media used for duckweed (*Spirodela punctata*) Muraleetharan *et al.,* (2013) and *Arabidopsis thaliana* treatment Nair *et al.,* (2014) , or sand matrix employed in wheat (*Triticum aestivum*) experiments Dimkpa *et al.,* (2013), compared to water treatment of broad bean (*Vicia faba*) Patlolla *et al.,* (2012) Fig.(39) , lettuce (*Lactuca sativa*), and cucumber (*Cucumis sativus*) Barrena *et al.,* (2009) . In algal research, significant agglomeration of uncoated AgNPs was also measured in high salt medium (HSM) used for *C. reinhardtii* cultures Dewez *et al.,* (2012) and BG-11 medium for *C. vulgaris* treatment Oukarroum *et al.,* (2012).

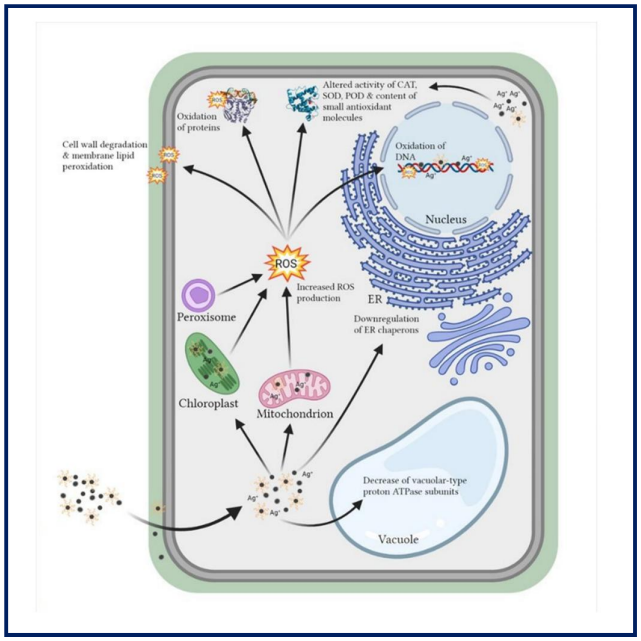

Fig. 39: Effect of differently coated AgNPs on plant and algal cells by direct interaction or through ROS formation. ROS reactive oxygen species, ER endoplasmic reticulum, CAT catalase, SOD superoxide dismutase, POD peroxidase. After Biba *et al.,* (2020).

Uncoated AgNPs have a negative surface charge due to the presence of hydroxo-, oxo-, or sulfide groups on the surface, which stabilizes them in deionized water. However, ex istence of counterions in the nutrient media and soil reduces repulsive forces between them and promotes aggregation Levard *et al.,* (2012). Stabilization of AgNPs in a medium can be achieved using surface coatings designed to lower their surface energy, prevent interactions with the environment, and diminish aggregation rates Ju-Nam and Lead (2008), Kvítek *et al.,* (2008). Different routes for AgNP stabilization can be employed, depending on their final application Cartwright *et al.,* (2020). Citrate, a small monomeric molecule Sharma *et al.,* (2014), Peharec *et al.,* (2018), Schubert *et al.,* (2018) is commonly implemented as a stabilizer in research of AgNP effects on plants and algae. It provides a highly negative charge at the AgNP surface, ensuring their stabilization through electrostatic means. Stability measurements of citrate-coated AgNPs in water medium using dynamic light scattering (DLS) revealed no significant changes in their size and surface charge in moderately hard water applied for maize (*Zea mays*) and cabbage (*Brassica oleracea*) treatment Pokhrel and Dubey (2013) . On the contrary, changes in AgNP zeta potential connected with the loss of coating and higher dissolution rates in ultrapure water were reported in an experiment with tobacco (*Nicotiana tabacum*) plants Peharec *et al.,* (2018). Most of researchers found citrate-coated AgNPs highly unstable in different media with high ionic strength used for plant growth. Significant increase in hydrodynamic diameter, indicating AgNP agglomeration, was observed in liquid half- and full-strength Murashige and Skoog (MS) medium Peharec *et al.,* (2021), Biba *et al.,* (2021), Ke *et al.,* (2018) , 1/4 Hoagland medium Geisler-Lee etal (2013) , and in a nutrient solution prepared according to OECD 221 guidelines Gubbins *et al.,* (2011) . Decreasing of zeta potential was also reported, indicating the loss of citrate coating Gubbins *et al.,* (2011), Li *et al.,* (2017). Moreover, significant concentrations of Ag^{+} ions were measured both in liquid nutrient media Ke *et al.,* (2018), Geisler-Lee *et al.,* (2013), Li *et al.,* (2010) and in soil Saleeb *et al.,* (2019), Lee *et al.,* (2012), because of citrate-coated AgNP dissolution. However, addition of natural polymers, such as Phytagel, stabilized AgNP-citrate in a solid MS medium by encapsulation, which reduced their oxidative changes during exposure of tobacco seedlings Biba *et al.,* (2021), Peharec *et al.,* (2018). On the other hand, AgNP-citrate seems to be quite stable in media used for cultivation of algae. No significant difference was obtained in size and zeta potential values in AgNP-citrate immersed in 10 mmol L^{-1} 3-morpholinopropanesulfonic acid (MOPS) used for Euglena gracilis treatment Yue *et al.,* (2017) , while

only minor dis solution was found in BG-11 medium used for C. vulgaris Qian *et al.,* (2019) . Generally, electrostatically stabilized AgNPs have shown less media-induced modifications when lower ionic strength and higher pH values are applied De Leersnyder *et al.,* (2016), Fernando and Zhou (2019) .

This could explain their higher stability in algal treatment media compared to media used in plant research. Surfactant molecules, such as positively charged CTAB, are also used in plant AgNP research as electrostatic stabilizers. As with AgNP-citrate, the behavior of AgNP-CTAB changes depending on the medium used for plant treatment and similar trends were observed. AgNP-CTAB was shown to be quite stable in ultrapure water used for treatment of onion (Allium cepa) roots Cvjetko *et al.,* (2017), but its addition in liquid 1/2 MS medium used for tobacco plants exposure led to rapid agglomeration observed by DLS measurements and transmission electron microscope (TEM) imaging. These findings were additionally corroborated by significant decrease of their zeta potential. Peharec *et al.,* (2021), Biba *et al.,* (2021), observed interesting trend with UV-VIS spectrometry in research, where AgNP-CTAB showed good stability in a solid 1/2 strength MS medium used for tobacco germination experiments. However, addition of cysteine, a strong silver ligand, led to rapid dissolution and release of Ag^{+}, indicating a fast removal of surface coating and showing that CTAB is a relatively labile ligand. The use of polymer coatings for AgNP stabilization provides a higher colloidal stability through steric repulsion between the polymer-coated particles Biba *et al.,* (2021), Schubert and Chanana (2018), Moore *et al.,* (2015), Mogoşanu *et al.,* (2016). The most frequently used polymer in plant and algal Nanotoxicology research is PVP Fig. (40).

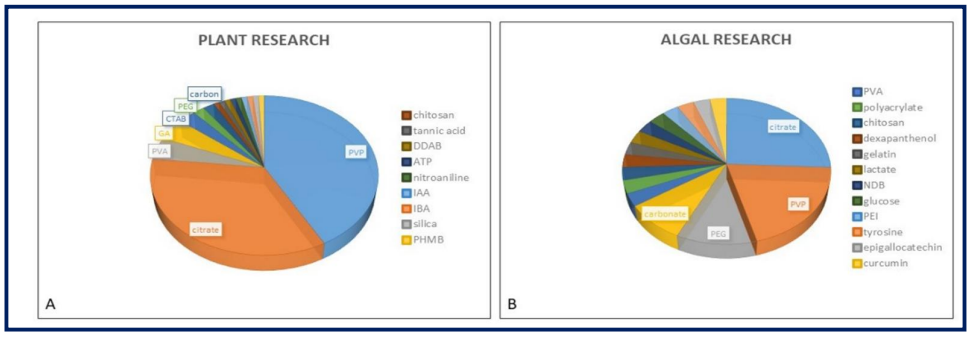

Fig. 40: Proportional representation of coatings used for AgNP stabilization in plant (A) and Algal (B) research. After Biba *et al.,* (2020).

High stability of PVP-coated AgNPs in plant research has been shown both in ultrapure water Cvjetko *et al.,* (2017) and in various nutrient media used for plant growth. The size of PVP-coated AgNPs was found to be constant in 1/2 Hunter's solution employed for Landoltia punctata two-day treatment Stegemeier *et al.,* (2017). Similarly, Jiang *et al.,* (2014) reported that 10% Hoagland's solution used for Spirodela polyrhiza treatment had no effect on AgNP-PVP shape and size, although their later research indicated a slight change in AgNP-PVP zeta potential in the aforementioned medium Jiang *et al.,* (2014). Yang *et al.,* (2019), Yang *et al.,* (2020), have examined how different environmental factors affect AgNP-PVP stability in media commonly used for growth of rice (Oriza sativa). Their results showed that chloride ions, which play an important role in uptake and accumulation of environmental silver (both particulate and ionic), significantly increase AgNP-PVP stability in Hewitt medium by increasing the overall negative charge of NPs, thus enhancing their dispersion Yang *et al.,* (2019).

Furthermore, their later research proved AgNP-PVP to be stable in 1/15 Hewitt medium even after the addition of Fe^{2+}- EDTA Yang *et al.,* (2020). On the other hand, a couple of studies have demonstrated medium-induced alterations of PVP-stabilized AgNPs. Comparison of DLS results for citrate-, PVP- and CTAB-coated AgNPs in 1/2 strength MS medium used for tobacco treatment showed a slower agglomeration rate for AgNP-PVP compared to AgNP-citrate and AgNP-CTAB, which was also accompanied by the decrease of their zeta potential Peharec *et al.,* (2021) . This finding indicated increased electrostatic repulsion between nanoparticles. In a similar study, AgNP-PVP were found to

be less stable and prone to dissolution in the solid 1/2 MS medium in comparison to AgNP- CTAB Biba *et al.,* (2020).

On top of that, addition of cysteine led to their rapid agglomeration coupled with additional dissolution and formation of silver clusters from dissolved Ag^+ Biba *et al.,* (2020). Stabilization of AgNPs by another type of steric molecule, GA, successfully protected AgNPs against aggregation and dissolution in ultrapure water used for treatment of Italian ryegrass (*Lolium multiflorum*) Yin *et al.,* (2011), and in 10% Hoagland medium used for exposure of *S. polyrhiza* Jiang *et al.,* (2012) , Jiang *et al.,* (2014) . Similar stabilizing capabilities were also observed for PEG-coated AgNPs that exhibited no significant changes in size in 1/4 Hoagland medium during A. thaliana treatment Wang etal (2013). Stability of polymer-coated AgNPs was also examined in algal research. PEG-, PVP-, and chitosan-coated AgNPs retained the same size and charge in MOPS used for C. reinhardtii treatment even after cysteine addition, confirming their excellent stabilization against dissolution in the medium Navarro *et al.,* (2015) . On the other hand, in a medium used for R. subcapitata cultivation and treatment, AgNP-PVP showed high agglomeration rate that was mitigated with the addition of a commercial humic substance, which provided electrostatic repulsive forces and decreased their zeta potential Wang *et al.,* (2015) . When three organic ligands with different numbers of phenol structures were used as AgNP coatings in toxicological studies on algae R. subcapitata, differences in their stability were observed in the Elendt M4 medium used for algal growth Lekamge *et al.,* (2020) . The highest rate of aggregation was obtained with tyrosine-AgNPs, followed by epigallocatechin gallate-AgNPs, while curcumin-coated AgNPs showed no signs of aggregation. Observed differences were attributed to different coating materials Lekamge *et al.,* (2020), proving that thorough characterization and stability analyses are imperative for accurate interpretation of nano-toxicological data. All these findings show that AgNP behavior in the nutrient media is far from predictable. This becomes even more complicated when plants or algae are added to the media. Interaction of AgNPs with the biomolecules present in biological environment (nucleic acids, proteins, lipids, etc.) can lead to the formation of the surface corona Argentiere *et al.,* (2016), Barrena *et al.,* (2009) that can reverse AgNP surface charge Lv *et al.,* .,(2019). These processes can either stabilize AgNPs or result in their increased aggregation and dissolution rates, depending on the AgNP intrinsic characteristics Akter *et al.,* (2018) Moore *et al.,* (2015). However, information on the AgNP corona formation in plant and algae is scarce due to the lack of published studies. Considering the emerging interest in application of nanotechnology in the agriculture Wheeler *et al.,* (2021) AgNP modifications due to the surface corona formation should be a focus of any future nano-toxicological studies.

11. Potential risk of AgNPs in human health.

Plants are producers in the ecosystem and represent the primary trophic level in the food chain. Regarding the food safety issue, most of the harvested edible tissues or organs of vegetables or cereals are consumed by livestock and humans. Nanomaterials can be taken up and accumulated in plants; they can further pose a risk to human health through invading the food chain and ultimately transferring to the human body. Several researchers, Monica and Cremonini (2009), Tripathi *et al.,* (2017), Tangaa *et al.,* (2016), Kalman *et al.,* (2015), reported that AgNPs could cycle in the ecosystem through various trophic levels in an aquatic or terrestrial food chain. Aquatic ecosystems, planktonic algae as primary producers are located at the base of the aquatic food chain; therefore, algae were selected as the basic trophic level to investigate trophic transfer of AgNPs in a few studies.

McTeer *et al.,* (2014) stated that bioavailability, toxicity, and trophic transfer of AgNPs between the alga Chlamydomonas reinhardtii and the grazing crustacean Daphnia magna, that belong to two different trophic levels. They also reported that Nano-Ag derived from AgNPs was accumulated into microalgae. After feeding on Ag-containing algae, Daphnia magna accumulated nano-derived Ag, confirming the trophic transfer of AgNPs between algae and Daphnia magna. Similar by, Kalman *et al.,* (2015) studied the bioaccumulation and trophic transfer of AgNPs in a simplified freshwater food chain comprising the green alga Chlorella vulgaris and Daphnia magna. After AgNPs were accumulated in algae, the Ag-contaminated algae were fed to Daphnia magna. Ag uptake in Daphnia magna was observed a few days later. Further analysis indicated that diet is the dominant pathway route of Ag uptake in Daphnia magna Kalman *et al.,* (2015).

In addition, a recent study used paddy microcosm systems to estimate the trophic transfer of AgNP-citrate and AgNP-PVP among various trophic level organisms (aquatic plants, biofilms, river

snails, and Chinese muddy loaches). After exposure, AgNPs rapidly coagulated and precipitated on the sediment. Park *et al.,* (2018), illustrated that stable isotope analysis indicated that their close correlation between the Ag content in the prey and that in their corresponding predators, demonstrating the impact of AgNPs on ecological receptors and food chains. In food chains, of terrestrial, studies on the potential trophic transfer of AgNPs remain scarce. However, the terrestrial trophic transfer of other metallic nanoparticles was investigated, such as AuNPs Judy *et al.,* (2012), CeO2-NPs Hawthorne *et al.,* (2014), and La2O3-NPs De la Torre Roche *et al.,* (2015). In a simulated terrestrial food chain, tobacco hornworm (Manduca sexta) caterpillars were fed tomato leaves that were surface-contaminated with AuNPs. Later, the transfer of AuNPs from tomato to tobacco hornworm was observed Judy *et al.,* (2012). These studies imply a possibility that AgNPs may also be transferred in the terrestrial food chains, in both in vivo and in vitro studies, which demonstrated the toxicity of AgNPs on mammalian cells. Sung *et al.,* (2008) reported that exposure of AgNP resulted in a reduction lung function and produced inflammatory lesions in the lungs of rat , and resulted in the accumulation of AgNPs in the olfactory bulbs and in the brain of rats Kim *et al.,* (2008). Since AgNPs can be accumulated and transferred in the food chain, they may become dangerous to humans. Exposure of AgNPs to human can stimulate inflammatory and immunological responses, because oxidative stress, and lead to cellular damage as reported by Luo *et al.,* (2015), Arora *et al.,* (2008). Therefore, there is an urgent need to increase our understanding of the bioaccumulation and trophic transfer of AgNPs in the food chain, which is critical for assessing and mitigating their potential harm to human health.

12. Conclusions and Future Prospects

Nanoparticles have recently been exploited in immense applications including agricultural system, but due to their size, toxicity, and reactivity with the several environmental factors, the dispersion and permeation of NPs into the ecosystem pose a challenge for the researchers. A great concern is arising related to the potential risk of human health, destruction in the ecosystem, decline in the food quality and yield due to AgNPs. Thus, the development of understanding about transfer of AgNPs through the ecosystem and their impacts on plants is of crucial importance. During the last decades, the researchers undertook the responsibility to increase the knowledge about the possible impacts of AgNPs on plants following various studies. Most of these studies revealed the detrimental effects of AgNPs on plants in various aspects including, anatomical, cellular, morphological, physiological, and molecular levels. However, few on the plants' growth and development also reported positive impacts of AgNPs. These contrasting results life-cycle based experimental system is required to accurately mimic the impacts of AgNPs on plants and to generate environmentally relevant implications. Most of the studies performed during the last decade focused on the morphological and physiological impacts of AgNPs on plant systems. However, profound impacts of AgNPs at the molecular level did not draw enough attention. Thus, more extensive and detailed studies are needed to explain the mechanisms and factors behind this unexplored research area. Therefore, systems biology and multiple omics methodologies (transcriptomics, proteomics, and metabolomics) can be employed in future studies to assess the phyto-toxicity and tolerance mechanisms of AgNPs and plants, respectively. indicated the complexity of the responses of plants to AgNPs, which are not only dependent on the properties of AgNPs (size, shape, concentration, source of Ag, and reducing agents, etc.) but are also determined by the plant system used (species, developmental stage, organ, tissue, etc.) and the methodology of experiments (exposure method, medium, exposure time, etc.). From various studies, it is clear that the NPs play divergent role and can positively or negatively influence the morphological or physiological traits of the plants. Different detoxifcation strategies were employed by different plant species to eliminate the toxic effects of AgNPs. Therefore, it is difficult to make a general conclusion about the tolerance mechanism of different plants species in response to AgNPs. To address this issue, it is necessary to use representative species, such as the commonly used model plant *Arabidopsis thaliana*, to evaluate the phyto-toxicity of AgNPs and tolerance mechanisms. Meanwhile, the establishment of a standardized protocol is required to conduct the experiments, thereby allowing comparisons between different plant species. Most of the experimental outcomes were based on controlled conditions (laboratory experiments), which are very different from feld conditions with respect to growing media (hydroponic vs. soil), treatment time (acute vs. chronic), and exposure dosage. Therefore, it is hard to predict the response of same plant species under two distinct growing conditions

(laboratory and field conditions) against exposure of AgNP. Consequently, the establishment of well-designed, plant.

Due to the immense application of AgNPs in various fields in modern society, their dispersal and permeation into the ecosystem became inevitable. Hence, a great concern is arising related to the potential risk of destruction in the ecosystem, decline in food quality and yield, and even undermining of human health imposed by AgNPs. To this concern, understanding how AgNPs transfer through the ecosystem and exert impacts on plants is of crucial importance. During the past decade, the research communities undertook the responsibility to increase our knowledge of the impacts of AgNPs on plants, by carrying out numerous studies regarding the interactions between plants and AgNPs. Most of these studies revealed the detrimental effects of AgNPs on plants in various aspects, including at morphological, physiological, cellular, and molecular levels. However, a few studies reported the positive effects of AgNPs on plant growth and development. These contradictory results indicate the complexity of the responses of plants to AgNPs, which are not only determined by the properties of AgNPs (size, concentration, shape, surface coating, Ag chemical form, etc.), but are also dependent on the plant system used (species, tissue, organ, developmental stage, etc.) and experimental methodology (medium, exposure method, exposure time, etc.) In response to AgNPs, it is rational that multiple detoxification strategies may be activated; different plant species may employ different detoxification mechanisms to eliminate the toxic effects of AgNPs. Therefore, it is difficult to make a general conclusion on how different detoxification pathways in response to diverse AgNPs conditions are activated in different plant species. To address this issue, it is necessary to use representative species, such as the commonly used model plant *s* to evaluate the phytotoxicity of AgNPs and tolerance mechanisms. Meanwhile, the establishment of a standardized methodology is required to conduct normalized AgNP exposure, thereby, allowing comparisons between different species. Although joint efforts by research communities generated essential knowledge of the impacts of AgNPs on plants, most of these experimental outcomes were based on laboratory experiments under controlled conditions that are likely far from field conditions, such as the exposure method (hydroponic vs. soil), exposure dosage, and time (acute vs. chronic).

Therefore, it is hard to predict whether the phytotoxicity of AgNPs and tolerance mechanisms under laboratory conditions are the same as under field conditions. To this end, the establishment of well-designed, plant life-cycle experimental systems under environmentally realistic conditions is required to accurately evaluate the impacts of AgNPs on plants and to generate environmentally relevant implications. In addition, most studies performed during the last decade focused on the impacts of AgNPs on plants at the morphological and physiological levels; however, the profound impacts of AgNPs at the molecular level did not draw enough attention. Benefits from the development of systems biology and multiple omics methodologies, such as transcriptomics, proteomics, and metabolomics, can be employed in future studies to comprehensively assess the phytotoxicity mechanism of AgNPs and tolerance mechanisms in plants.

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