



Translocation and transformation of engineered nanomaterials in plant cells and their effect on metabolism

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Abstract: As the climate worsens and the demand for food grows, so does the interest in nanoagriculture. The interaction between plants and nanomaterials (NMs) has been extensively and intensively examined. However, stopping at the outcome of a phenomenon is often insufficient. Therefore, we introduce three important processes of nanoparticle-plant interactions: translocation, transformation, and plant metabolism. During the migration of nanoparticles, size and surface electrical properties are the main determining factors. Additionally, the interaction of nanoparticles with cell membranes is another key aspect of research. The transformation of nanoparticles in plants is mainly due to redox substances. The way that nanoparticles affect plant metabolism may be able to shed light on the interaction of nanoparticles with plants. This review adds to the existing knowledge on the design of nanoagrochemicals and summarizes the mechanism of interaction of NMs with plants. In this way, NMs can be used for their beneficial effects and thus contribute to the maintenance of food security and sustainable development.

Introduction

As the population continues to grow, the demand for food gradually increases. By 2050, the demand for food will rise by 70% (Bindraban *et al.*, 2018). In the face of food needs and security, nanomaterials (NMs) emerge as a promising solution. Traditional agrochemicals cause some environmental pollution, and although they are of great help to agricultural production, the cost is also unaffordable for people. Climate degradation is also urging an accelerated exploration of nanotechnology applications in agricultural environments. Currently, the NMs are used in a number of environmental applications, including the reduction of air pollution (Lou *et al.*, 2022; Zhao *et al.*, 2022b), mitigation of heavy metal stress (Zhou *et al.*, 2021b), and water purification (Chong *et al.*, 2010; Jjagwe *et al.*, 2021). The more thorough investigation has also inadvertently assisted in the understanding of NMs' effects on plant physiology (Faizan *et al.*, 2021; Iannone *et al.*, 2014; Juárez-Maldonado, 2022;

Juárez-Maldonado, 2022). It has been demonstrated that NMs can encourage plant development and enhance the condition of plants' growth (Adeel *et al.*, 2021; Farooq *et al.*, 2021; Li *et al.*, 2021; Pang *et al.*, 2021; Shakoore *et al.*, 2022; Wang *et al.*, 2020). However, NMs are like two sides of the same coin, and some studies have pointed out that NMs may have adverse effects on plants under certain conditions (Bai *et al.*, 2021; Guo *et al.*, 2022; Wang *et al.*, 2019). Excessive amounts of NMs can be toxic and hinder the growth and development of soil microorganisms and plants (Chen *et al.*, 2022; Dev *et al.*, 2018; Li *et al.*, 2022; Sardoiwala *et al.*, 2018; Yusefi-Tanha *et al.*, 2022; Zhao *et al.*, 2022a). The accumulation of NMs in the environment poses a concern to the human body since they can enter through a number of different channels (Moore, 2006; Sharifi *et al.*, 2012; Zhang *et al.*, 2018).

Understanding the biological impacts of NMs on plants requires an understanding of their transport, change, and impact on plant metabolism (Lin *et al.*, 2009; Schymura *et al.*, 2017). The application of NMs includes foliar, root application, and seed germination (Wang *et al.*, 2022d; Yue *et al.*, 2022; Zhao *et al.*, 2020). The NMs migrate into the plant, which has been explored in depth in a previous review

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(Dietz and Herth, 2011; Lv *et al.*, 2019; Siddiqi and Husen, 2017; Singh *et al.*, 2018; Usman *et al.*, 2020; Verma *et al.*, 2019). We are especially interested in the migration of NMs at the cellular level (Gao *et al.*, 2019; Hua *et al.*, 2021; Qu *et al.*, 2022), which has gotten less attention. The size of the nanoparticles (NPs), which are the main barriers to NM entrance into plant cells, has the biggest impact. The barriers to entry of NPs into plant cells mainly consist of cell walls and membrane structures. The charge carried by NPs and cell wall and membrane structures is also one of the factors worth considering (Hu *et al.*, 2020). We will describe it in detail below. The migration is accompanied by the transformation of NPs, and the transformation also facilitates the migration of elemental species to some extent. For example, in ZnO NPs as nanopesticides, the Zn^{2+} ion exhibits the antibacterial effect. Reactive oxygen species (ROS) that have a sterilizing effect, are also produced by ZnO NPs (Khan *et al.*, 2016; Molnár *et al.*, 2020; Wagner *et al.*, 2016). The entry of NPs into plants also affects plant metabolism indirectly through phytohormones and light and efficiency, which will be described in detail here.

We searched the *web of science* using the subject terms (1) “plants” and “nanomaterials” and “transfer”; (2) “plants” and “nanomaterials” and “transformation”; (3) “plants” and “nanomaterials” and “metabolism”. A total of 70 reviews were screened, and keyword co-occurrence analysis was

performed on these 70 reviews (Fig. 1). In the co-occurrence illustration (Fig. 1), we could draw some conclusions from the current reviews: (1) There are only a few reviews on the effects of the migration transformation process of nanoparticles; (2) Applications for nano-agriculture, such as nano-fertilizers and nano-sensors, are increasingly becoming research topics of interest; (3) Engineered nanomaterials have a large body of research and are a major research target for studying plant-nanomaterial interactions.

This review introduces the migration, transformation, and influence of NPs on plant metabolism (Fig. 2). The mechanisms of these processes and the factors affecting the migration and transformation of NPs were explored, and challenges and future research directions are highlighted. The novelty of this paper lies in the overview of the important activities faced in the internalization of nanoparticles and the presentation of the process from the outside to the inside of the plant system. This review thus sheds light on the current research on NPs at the plant cellular level.

The Translocation of Nanomaterials in Plant

NMs are structurally prevented from entering the plant cell walls and membranes. NPs also interact with the elements of the cell wall and membrane. For the design and

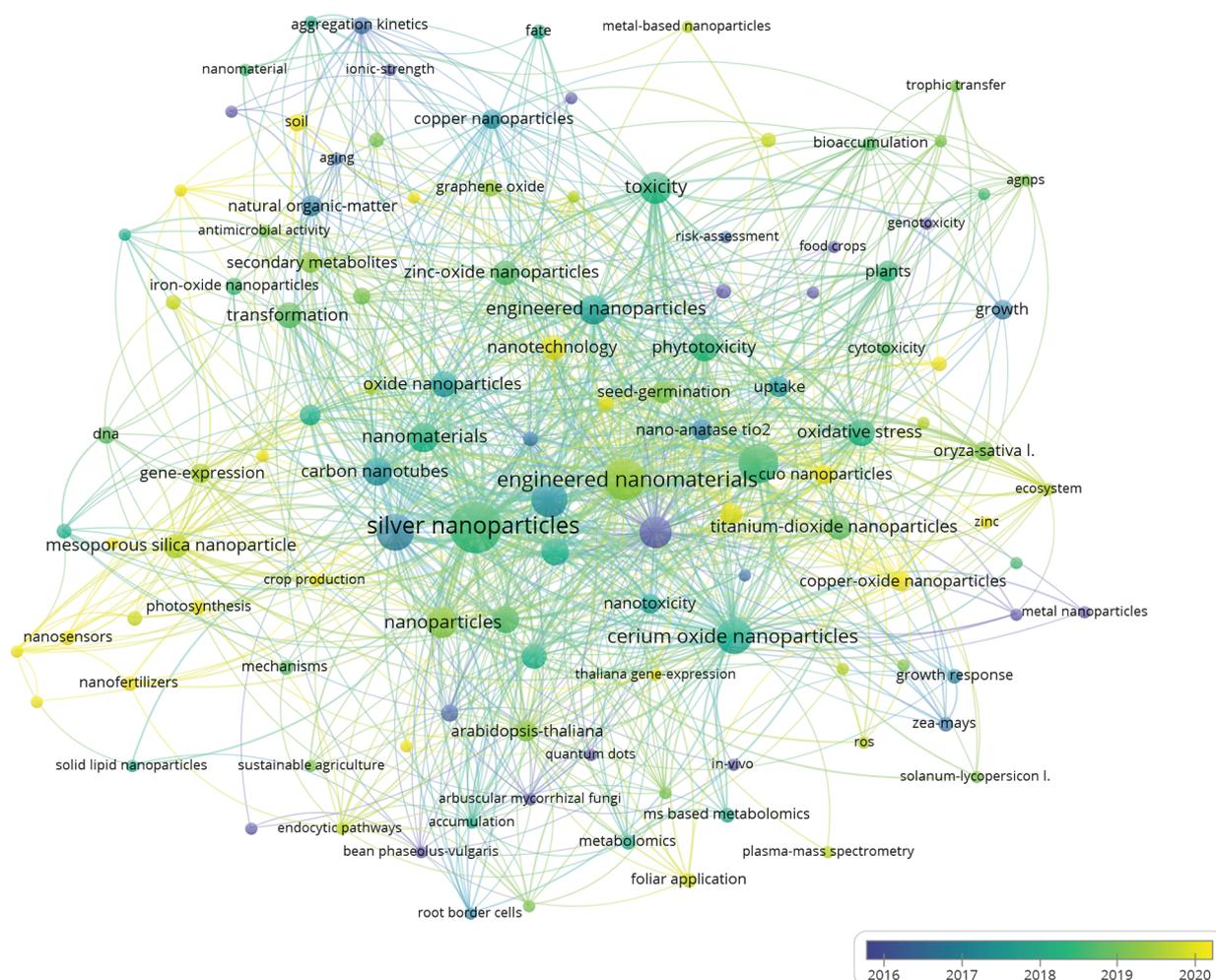


FIGURE 1. An illustration of co-occurrence analysis of a review on nanomaterial migration, transformation, and impact on plant metabolism.

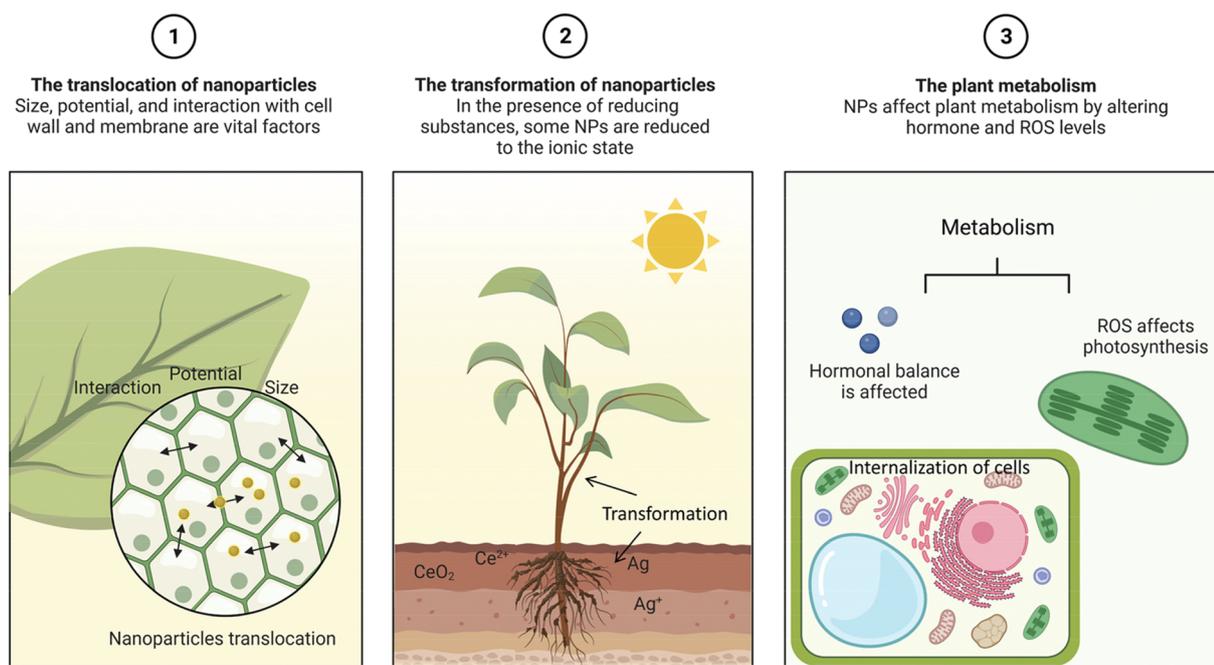


FIGURE 2. Illustration of the variables that affect plant metabolism, nanoparticle translocation, and nanoparticle transformation.

application of NPs, it is crucial to investigate the challenges and influencing factors encountered during the migration of NPs (Fig. 3). We will next discuss the structure of plant cells from the outside to the inside, in terms of the cell wall dimensions, the interaction of NMs with the cell wall and the interaction of NMs with the membrane structure in turn.

The pore size of plant cell wall

The cell wall is a more solid, durable, and slightly more flexible structure than the cell membrane. Cellulose, hemicellulose, and lignin make up the majority of the cell wall (Zeng *et al.*, 2017). Plant cells must face the engineered nanomaterials before they may enter the cell. Plant cell walls are made up of a cross-linked network of pectins and proteins (Shomer *et al.*, 2003). Also, the cross-linked network determines the

size of the wall pores of dicotyledonous cells (Fleischer *et al.*, 1999). The size of the cell wall prevents NMs from migrating further (Wu and Li, 2022). Therefore, it is crucial to comprehend the size of the cell wall pores (Carpita *et al.*, 1979; Lew *et al.*, 2018). For different plants, the porosity tends to differ (Chesson *et al.*, 1997; Fujino and Itoh, 1998). The radius of the wheat (*Triticum aestivum* L.) cell wall pores is 1.5–3 nm (Chesson *et al.*, 1997). The pore size of maize (*Z. mays* L.) stover cell walls is between 10 and 1000 nm, although it varies depending on where it is located (Chundawat *et al.*, 2011). In one experiment, 11 nm NPs were discovered on the leaves of the maize (Hu *et al.*, 2020). The epidermal cells of the pea (*Pisum sativum*) feature pores that are typically 5.5 ± 1.4 nm in size for their elongating cell wall and 13.4 ± 4.3 nm for their

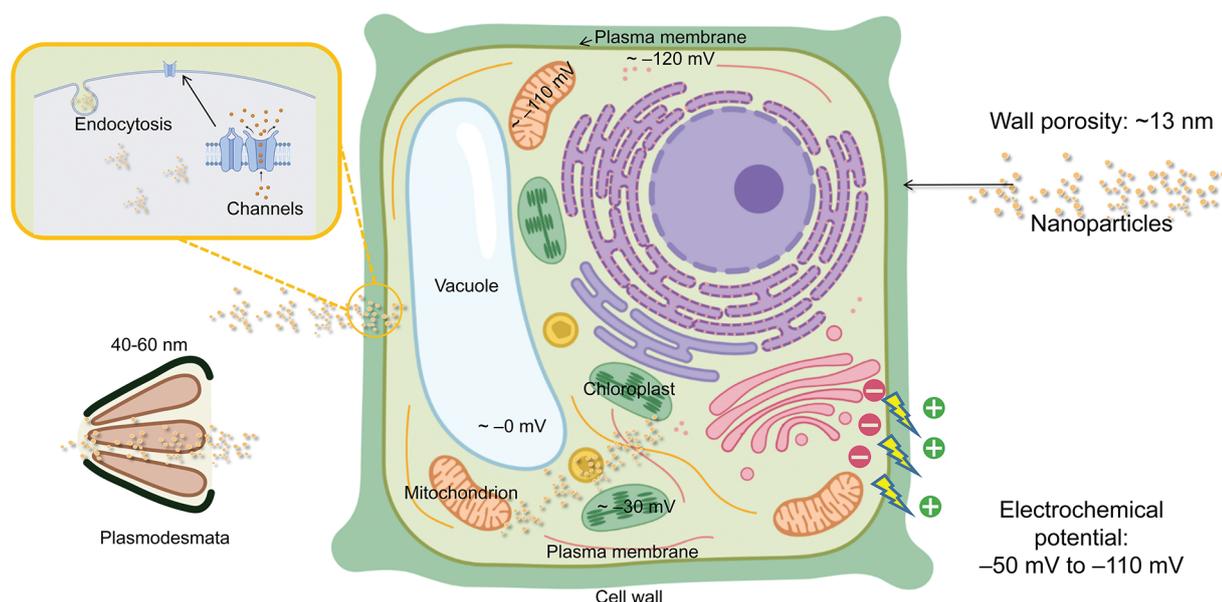


FIGURE 3. Illustration of possible barriers to the entry of NPs into plant cells.

non-elongating cell wall (Fujino and Itoh, 1998). The STEM examination of NPs isolated from leaves revealed a 10 nm-diameter of Zr/CeOx NPs (Schwabe et al., 2015). When the particle size was more than 20 nm, no root-to-shoot translocation was seen. The same outcomes of a second experiment demonstrated that 18 nm size Fe₂O₃ NPs could not be transported from roots to shoots of maize (Li et al., 2016).

In general, NPs smaller than 13 nm in size are able to enter plant cells directly through cell wall pores, while those with larger sizes, such as 40–60 nm, can enter plant cells through intercellular filaments.

The interaction between nanomaterials and the cell wall

The ability of NMs to pass through the cell wall may be influenced by elements other than the size of the cell wall pores. There may be more complex interactions between the NMs and the cell wall.

Transmission electron microscopy studies suggest that the root cell wall of Brassica (*Brassica napus*) treated with ZnO NPs at a concentration of 25 mg/L was bound to Zn²⁺ (Molnár et al., 2020). This demonstrates the capacity of ZnO NPs to modify cell membranes. Because plant cell walls are active, they can easily redesign themselves in response to environmental changes (Houston et al., 2016). After being exposed to Y₂O₃ NPs, the form and composition of cell wall of tobacco (*Nicotiana tabacum* L.) were also altered. The cell wall thickness of tobacco increased significantly by 7–12 times, the pectin content increased by 58%, and the hemicellulose content decreased by 29% (Chen et al., 2021). In the presence of ROS, Ag⁺ produced by Ag NPs can bind to hydroxy cellulose structures, breaking hydrogen bonds to promote changes in cell wall structure (Pinheiro et al., 2021). Pea (*Pisum sativum* L.) growth exposed to TiO₂ NPs exhibited altered polysaccharide content of the cell wall (Fan et al., 2014). Similar to this, Fourier transform infrared spectroscopy studies revealed that TiO₂ NPs altered the composition of the leaf cell walls of tomatoes (*Solanum lycopersicum* L.). The alterations in the amounts of xyloglucan and hypergalacturonic acid were validated by microarray polymer analysis (Line et al., 2021). Another intriguing study looked at nZVI's potential to encourage root growth in Arabidopsis (*Arabidopsis thaliana*). The concentration of 0.5 g/L nZVI increased root elongation by 150%–200% via inducing OH radical-induced cell wall loosening and the beginning of H₂O₂ release (Kim et al., 2014).

Electrical characteristics based on pore size are the second most crucial component to take into account. In a previous study, maize leaves were exposed to positively and negatively charged NPs on their surface, but their size was larger than 11 nm, which possibly limited their access to the interior of the plant (Hu et al., 2020). The electrical potential of the cell wall is another factor that must be considered. The electrical charge in the cell wall is typically between –50 and –110 mV (Shomer et al., 2003). The NPs with a charge opposite to that of the cell wall may be retained by the cell wall (Bao et al., 2016; Juarez-Maldonado et al., 2019). Negatively charged Au NPs were found in the roots of Arabidopsis (*Arabidopsis thaliana*), and positively charged Au NPs were not detected in the roots cell (Avellan

et al., 2017). Negative polarity Se NPs were more abundant in the Bok Choy (*Brassica chinensis* L.) shoots (Wang et al., 2022b). This also shows that negatively charged cell walls may play a role in the retention of positively charged NPs in roots, thus giving us ideas for the creation of nanopesticides or nanofertilizers in the future. Positively charged NPs, on the other hand, appear to be better at moving within plants, according to some studies. Indeed, the positively charged ZnO NPs allowed their adsorption on the leaf surface and cell walls and were more uniformly distributed within the leaf than the negatively charged ones (Zhu et al., 2021).

NMs have also been shown to alter the composition of cell walls. As mentioned previously, Y₂O₃ NPs can alter the pectin and hemicellulose content of plant cell walls (Chen et al., 2021). CuO NPs also reduced the amount of cellulose, hemicellulose, pectin, and other monosaccharides in the tomato (*Solanum lycopersicum* L.) root cell wall (Jia et al., 2022). Molnár et al. (2020) discovered that NP concentrations must exceed a specific threshold to modify the structure of the cell wall.

The role of cell wall potential in the uptake of NPs by plants and whether or not interactions between NPs and plant cell walls are connected with different cell types are both poorly understood. As a result, we must consider factors including the electrical gradient across the cell wall, NP size, interactions with cell wall components, and NP concentration that also influence NP movement inside the plant.

The interaction between nanomaterials and the membrane

NPs must overcome the membrane barrier after passing through the cell wall (Wu and Li, 2022). The plasma membrane, a border membrane that encloses the contents of the cell, is normally 5–10 nm thick. Some of the methods of cellular internalization include endocytosis, penetration through transporters or channels in the cell membrane, and lipid exchange envelopes (Lv et al., 2021; Perozo et al., 2002; Schwab et al., 2016; Sosan et al., 2016; Wong et al., 2016; Wu et al., 2017).

Similar to plant cell walls, the membrane potential plays a crucial role in controlling the flow of NPs through the membrane (Wu and Li, 2022). The plasma membrane potential is greater than that of the cell wall, at roughly –120 mV (Wu et al., 2013). High-zeta potential NPs are capable of entering protoplasts (Lew et al., 2018). However, it has been found that Au NPs crossing the plasma membrane are not affected by their electrical properties (Milewska-Hendel et al., 2019). The usage of 5 nm Au NPs, which are within the range of passing size for the channels on the plasma membrane, may be the cause of this. NPs are also able to infiltrate organelles other than protoplasts by traversing organelle membranes (Liu et al., 2021; Milewska-Hendel et al., 2019; Wu et al., 2017; Zhou et al., 2021a). The interaction of NPs with membranes has received little attention, although it might be one of the most intriguing areas for future study.

The Transformation of Nanomaterials in Plant

In the plant, the NPs may undergo transformation (Table 1), producing a number of elemental species (Lv et al., 2019). This

TABLE 1

Transformation process of nanoparticles in plants

Nanoparticles	Plant	Transformation products	Reason	Ref.
Ag NPs	Wheat (<i>Triticum aestivum</i> L.)	Ag ⁺	Dissolution	(Larue <i>et al.</i> , 2014)
ZnO NPs	Desert plant (<i>Prosopis juliflora-velutina</i>)	Zn-nitrate, Zn-phosphate, and Zn-citrate	Redox species	(de la Rosa <i>et al.</i> , 2011)
CeO ₂ NPs	Cucumber (<i>Cucumis sativus</i> L.)	CePO ₄	Redox species	(Zhang <i>et al.</i> , 2012)
CeO ₂ NPs	Head lettuce (<i>Lactuca</i>)	Ce ³⁺	Redox species	(Zhang <i>et al.</i> , 2015)

process is mainly due to (1) root secretions or (2) the interaction of biofilms around the root system, and (3) redox species in the plant.

After being adsorbed on the surface of plant roots, NPs undergo oxidative solubilization to pass the cell membrane, and after internalization, NPs can move within and across plant tissues. X-ray spectro-microscopy revealed that Ag NPs were oxidized within the root tissue of *Lolium multiflorum* (Yin *et al.*, 2011). Ag NPs are oxidized directly inside the root tissue or are oxidized, and the Ag⁺ is absorbed by the roots. Alfalfa sprouts can absorb Ag⁺ from the culture medium and reduce it to Ag NPs in their bodies. Alfalfa plant tissues contain the accumulated Ag atoms that undergo processes related to nucleation and NPs production (Gardea-Torresdey *et al.*, 2003). Similarly, Au underwent a reduction reaction in alfalfa plants to produce Au NPs (Gardea-Torresdey *et al.*, 2002). At that time, these findings were very interesting and may provide some new inspiration for the development of green synthetic NPs (Jiang *et al.*, 2022). The metal oxides can vary in a way that affects plant accumulation and species creation. When treated with ZnO NPs, the roots and shoots of the maize plant absorb Zn predominantly in ionic form. The biotransformation of ZnO NPs into ZnO phosphate in the plant limits their long-distance transport since there is relatively little upward migration of Zn in the shoots (Lv *et al.*, 2015). CuO and Cu (I)-sulfur complexes are the main forms of bioaccumulated copper in wheat (*Triticum aestivum* L.), whereas the phosphate form is the main form of bioaccumulated Zn (Dimkpa *et al.*, 2012). This is principally brought upon by an increase in the solubilization of ZnO NP between the roots as well as plant uptake and translocation of Zn ions (Lv *et al.*, 2015). Zn was discovered in soybean (*Glycine max*) root tissue as Zn-nitrate and Zn-acetate (Lopez-Moreno *et al.*, 2010). In subsequent experiments, Zn-citrate was detected by the mu-XANES technique (Hernandez-Viezcas *et al.*, 2013). Similarly, different forms of Zn were also found in other plants (Hernandez-Viezcas *et al.*, 2011; Wang *et al.*, 2013). Despite the presence of numerous Zn species in the plants under study, it is clear that Zn uptake, transport, and accumulation in plants primarily take place in the form of Zn²⁺ produced by ZnO NPs (Lv *et al.*, 2019). The CuO NPs and ZnO NPs are the NPs with more applications in agriculture (Wang *et al.*, 2022c). Zn uptake, transport, and accumulation in plants happen largely in the form of Zn²⁺ released by ZnO NPs, although many Zn species were found in the plants under study (Dimkpa *et al.*,

2012). In maize, CuO NPs move from the branches back to the roots through the bast, where they can be converted to Cu(I) (Wang *et al.*, 2012). While a portion of the dissolved Cu(II) was also reduced to Cu₂O, it was mostly coupled with ligands like cysteine, citrate, and phosphate. Additionally, rice roots were found to transfer 40 nm CuO NPs to the shoots (Peng *et al.*, 2015). In cucumbers exposed to CeO₂ NPs, Ce occurs as CeO₂ and CePO₄ in the roots and as CeO₂ and Ce-carboxylic acid in the branches, according to XANES spectra (Zhang *et al.*, 2012). The primary causes could be (1) the function of ascorbic acid as a reducing agent and (2) the organic acids-mediated dissolution of CeO₂ NPs. Other tests have shown similar outcomes (Cui *et al.*, 2014; Hernandez-Viezcas *et al.*, 2013). Plants cultivated hydroponically had NPs on their root surfaces (Martinez-Fernandez and Komarek, 2016). CeO₂ NPs must physically come in contact with root secretions at the nanobeneficial interface for them to convert into ionic form in plants (Ma *et al.*, 2015). The shape of NPs may also have an impact on conversion; NPs and nanocubes have higher surface reactivity than nanowires, leading to increased Ag⁺ release and toxicity (Gorka and Liu, 2016). Rod-shaped CeO₂ NPs converted Ce³⁺ to a higher extent than other CeO₂ NPs, demonstrating that rod-shaped NPs are the most chemically reactive (Zhang *et al.*, 2017).

The transformation of NPs by plants has been extensively studied. Redox compounds are the main cause of NP transformation in plants. Accordingly, our examination of the biological concepts underpinning the impacts of NPs on plants will thus have a framework to work on. Additionally, this framework promotes the use and development of nanotechnology in agriculture, which could provide direction for further study.

The Effect of Nanomaterials on Metabolism in Plant

Often, more than one pathway participates in various aspects of plant metabolism. For example, glycolytic pathways and pentose phosphate pathways are involved in carbohydrate degradation; five different pathways participate in electron transfer in the respiratory chain, and electrons can be transferred to oxygen through a variety of terminal oxidases. Different metabolic pathways exist simultaneously in plants, but they do not operate at equal rates, and the ratio between rates is not fixed. Which metabolic pathway a plant employs in a given environment—and how different the pathways

are—depends on the plant species, the organ, the stage of growth and development, and the environment.

The oxidative burst can be caused by NPs interfering with a variety of oxidative processes in plants, but they can also provide micronutrients, control gene expression, or perform all of these functions (Hossain *et al.*, 2015; Liu and Lal, 2015; Nair and Chung, 2014). NPs can affect plant hormone levels. The increase in cytokinin level in pepper under Ag NPs stress and the decrease of IAA and ABA in cotton (*Gossypium spp*) under CuO NPs stress indicated that the NPs affect the hormone balance in plants, which in turn affect the metabolic processes in plants (O'Brien and Benkova, 2013). Following Y₂O₃ NPs stress, transcriptome analysis showed that genes involved in cell wall metabolism and remodeling undergo considerable alterations (Chen *et al.*, 2021). NPs also influence ROS production, and electron transport in mitochondria and chloroplasts is affected by excess ROS. Photosynthesis is the only source of energy for plants; thus, mitochondria and chloroplasts have an impact on every aspect of plant metabolism and physiology (Foyer and Shigeoka, 2011; Kalaji *et al.*, 2014). Based on the association between ROS and secondary signaling messengers, which results in transcriptional regulation of secondary metabolism, it has been determined that ROS produced during interactions with NPs may interfere with secondary metabolism in plants (Marslin *et al.*, 2017). The metabolism of plants is similarly affected by the dosage effect of NPs. The secondary metabolism of the bean (*Phaseolus vulgaris* L.) roots and leaves was severely impacted at relatively low dosages (0, 25, 50, and 100 mg/L) of CeO₂ NPs treatment (Salehi *et al.*, 2020). In another report, carbon dots successfully improved soybean photosynthesis during a drought. The increase in photosynthesis had a big impact on agricultural yield and quality as well as growth and development (Wang *et al.*, 2022a).

Generally speaking, NPs change the levels of hormones and ROS in plants, which affects their metabolic activities among the key physiological functions of plants. Studying the effects of NPs on plant metabolism can reveal the responses made by plants exposed to NPs.

Conclusion and Perspective

In this review, we present the entry, migration, transformation, and metabolism of NPs in plants. The main factors affecting the migration transition of NPs are their size and surface charge. The transformation process of NPs is mainly caused by three factors, including (i) plant root secretions; (ii) biofilm interactions; and (iii) redox substances in plants. Current studies on size have found that nanoscale properties are predominant for particles below 30 nm. The current research on the size of NPs is getting more exhaustive. Plant hormone and ROS production may be impacted by NPs; plant hormones have an impact on a plant's metabolism, and too many ROS prevent photosynthesis, which in turn affects metabolic processes in a plant.

Future research should consider the following points: (1) NMs may be modified to undergo surface modifications that alter the charge on their surface, facilitating the passage through organelle membranes; (2) Targeted transport of

nanocarriers in plants is an interesting hypothesis (Miyamoto *et al.*, 2022), which may provide good ideas for future targeted application of nanopesticides; (3) More studies need to examine the pathway and the amount of NPs entering the plant.

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