PLANT SCIENCE TODAY
Vol 12(sp4): 01–08
https://doi.org/10.14719/pst.10404

eISSN 2348-1900

REVIEW ARTICLE

Mechanisms involved in the uptake of nanofertilizers in the soil-plant system: A review

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Received: 02 July 2025; Accepted: 25 August 2025; Available online: Version 1.0: 05 November 2025

Cite this article: Dhara H, Rathod S, Timothy L, Tirtharaj P, Kenny Z, Tasvina RB, Helim R. Mechanisms involved in the uptake of nanofertilizers in the soil-plant system: A review. Plant Science Today. 2025;12(sp4):01–08. https://doi.org/10.14719/pst.10404

Abstract

To meet the demands of a projected population of nine billion people by 2050, a minimum 50 % increase in food production requires advanced technological interventions, considering the increasing deterioration of water and land resources. Nanotechnology initiatives have been launched to improve the agricultural sector, taking into account the exceptional properties of nanoparticles. The increasing application of nanotechnology in agriculture relies on several factors, including established effects, potential toxicity, monitored environmental fate and overdose thresholds. Plants are integral to ecosystems and nanoparticles can interact with their environment, including plant systems. Nanoparticles can engage with plants, affecting their absorption and accumulation in plant biomass, hence modifying their environmental fate and movement. Nanoparticles can penetrate living plant tissues. This has significant implications for their aggregation behaviour in ecosystems and their potential role as intelligent delivery systems within plants. Determining the ability of plants to absorb and transport intact nanoparticles is essential for various plant tissues. Precise dosage and effectiveness of nanoparticles on plant target surfaces represent a significant challenge. Minimising the dispersion of chemical products from bulk materials, such as mineral fertilisers, has emerged as a beneficial characteristic that enhances the possible application. To govern the role of nanoparticles within and outside of plants and their environmental implications, rigorous research under controlled settings is essential. Formulating an application strategy requires a thorough evaluation of nanoparticle dosage, exposure duration, translocation and accumulation patterns and mechanisms of action within plants.

Keywords: accumulation; nanoparticles; nutrients; translocation; uptake

Introduction

The world will need to increase food production by 50 % by 2050 if it is to meet the nutritional needs of 9 billion people (1). This necessitates innovative technical interventions, given the growing scarcity of land and water. Nanotechnology, owing to the unique properties of nanoparticles, has emerged as a promising tool to enhance agricultural productivity. Various nanoparticles, including ceramics, metal oxides, silicates, magnetic materials, polymers, lipids, dendrimers and emulsions are used to improve nutrient delivery, reduce the need for plant protection products (PPP) and ultimately increase agricultural income (2). Critical concerns include dosage levels, known biological effects, potential toxicity and environmental fate. Nanoparticles may interact with their environment and plants are an integral part of any ecosystem. As a result, it is safe to say that nanoparticles can have interactions with plants, which can impact their environmental fate and transit via processes such as ingestion and accumulation in plant biomass. The ability of nanoparticles to penetrate plant tissues has critical implications for their environmental aggregation behavior and their efficacy as smart delivery systems within plant systems. Understanding whether plants can uptake intact nanoparticles and translocate them is essential. Entry points may include root junctions, wounds, cuticles, stomata, hydathodes, trichomes and internal root tissues.

Recent reports in plant science indicate that nanoparticles enhance agronomic capacities like photosynthetic rate, respiration, number of leaves, leaf area index, etc. Beyond their application as herbicides, insecticides and sensing materials, nanoparticles have the potential to improve plant nutrition and act as carriers for the controlled release of agrochemicals (3). Furthermore, nanoparticles enhance plant tolerance and accelerate adaptability to diverse climatic changes. Certain nanoparticles, exhibiting distinctive physiochemical properties, inherently promote plant development and augment stress tolerance, rather than only serving as nanocarriers. The physicochemical properties of nanoparticles, the application methods (soil, foliar and hydroponics) and the amounts employed all affect their biological activity. *In vitro* plant tissue cultures have shown that nanoparticles significantly affect callus induction, organogenesis, somatic embryogenesis and secondary metabolite synthesis. Although the process remains ambiguous, these findings suggest that plant cells can uptake nanoparticles via their cell walls. Recent years have witnessed substantial advancements, building upon previous research regarding the application of nanoparticles for DNA transport in plant cells (1).

Nanoparticles are colloidal structures of between one and one hundred nanometers in size. They display unique traits that define enhanced chemical, optical, mechanical and electrical capabilities, featuring an extraordinarily high surface-to-volume ratio and specific surface area. Nanoparticles constitute a diverse assortment of materials in terms of their structure and chemical composition. The materials include semiconductors, metal oxides, lipids, carbonaceous compounds, zero-valent metals, quantum dots, nanopolymers and dendrimers, presented in diverse configurations such as rods, fibres, wires and sheets (4, 5). In addition to enhancing fertiliser usage efficiency, minimising volatilisation and leaching and mitigating environmental concerns, appropriately applied nanoparticles can provide controlled and gradual nourishment to plants.

Translocation and Absorption of Nanoparticles

Mechanisms of nanoparticle uptake in plants

The toxicity and bioavailability of nanoparticles are influenced by a series of biological and geochemical transformations that take place within the soil environment. Upon interacting with the plant's roots, the nanoparticles ascend to the aerial regions and accumulate within the cellular or subcellular organelles (6). Several studies have indicated that this process is mediated by factors such as crystal phase dissolution, biotransformation and changes in nanoparticle speciation, which facilitate their uptake and internal movement (1). The dimensions of nanoparticles play a pivotal role in facilitating their ingress through plant stomata or the pores of cell walls, thereby establishing a direct correlation with their absorption capabilities. Furthermore, the dimensions of these entities play a crucial role in determining their toxicity, accumulation and transport kinetics into plant cells, thereby influencing subsequent transport mechanisms into cellular structures such as plasmodesmata or organelles (7).

Additionally, nanoparticle morphology, including surface structure, surface charge and aggregation behaviour, plays a central role in their interaction with plant cells (8). Since plant cell walls are negatively charged, positively charged nanoparticles show stronger binding affinity (7). Nanoparticle size and surface structure help define their specific interaction sites within plant cells (9). The attachment of nanoparticles to the surface of plant cells is fundamentally influenced by their charge, given that the cell wall is inherently negatively charged (7).

In addition to particle size and surface charge, the hydrophobicity of plant surfaces plays a significant role in determining the absorption and translocation of nanoparticles (10). Moreover, evaluating the influence of nanoparticles on absorption, transport and aggregation within plants serves to enhance our understanding of their intrinsic structure. The previously mentioned facts underscore the importance of standardising laboratory tests to assess nanoparticles in plant tissues across varying concentrations, thereby enabling a precise determination of the impact of nanoparticles, supported by their physical-chemical properties (11). Consequently, an exhaustive examination of the characteristics of the nanoparticles is essential to understand and elucidate the processes of absorption, translocation and accumulation (12). Advanced imaging and analytical techniques should be employed to precisely trace their movement and distribution within plant structures and organelles (Fig. 1).

Nanoparticles ranging from 3 - 5 nm in size have shown the ability to penetrate plant roots through mechanisms such as capillary forces, osmotic pressure or direct passage through the root epidermal cells (13). The semipermeable epidermal cells of the root cell wall include minute pores that exclude large nanoparticles (14). Specific nanoparticles (ZnO, TiO_2, SiO_2 and FeO etc.) increased the permeability of the epidermal cell wall, facilitating their entry. Upon traversing the cell walls, nanoparticles are apoplastically transported across extracellular spaces until they reach the central vascular cylinder, facilitating unidirectional ascent inside the xylem (15). Nanoparticles must symplastically navigate the Casparian strip barrier to reach the core vascular cylinder. This is accomplished through the binding of carrier proteins in the endodermal cell membrane via endocytosis, pore creation and transport. Ultimately, this enables their systemic distribution throughout the plant via the vascular system.

Nanoparticles can move between cells through plasmodesmata and cytoplasmic channels connecting adjacent cells. At the Casparian strip, nanoparticles that cannot cross into the symplast tend to aggregate, while those that successfully enter the xylem are transported to aerial parts of the plant and may later return to the roots via phloem circulation (9). Nanoparticles that plants absorb may be present in the cytoplasm of cortical cells, the nucleus and the epidermal cell wall. Nutrient absorption may be modified by nanoparticles that do not adhere to the root surface of the soil aggregate (Fig. 2, 3).

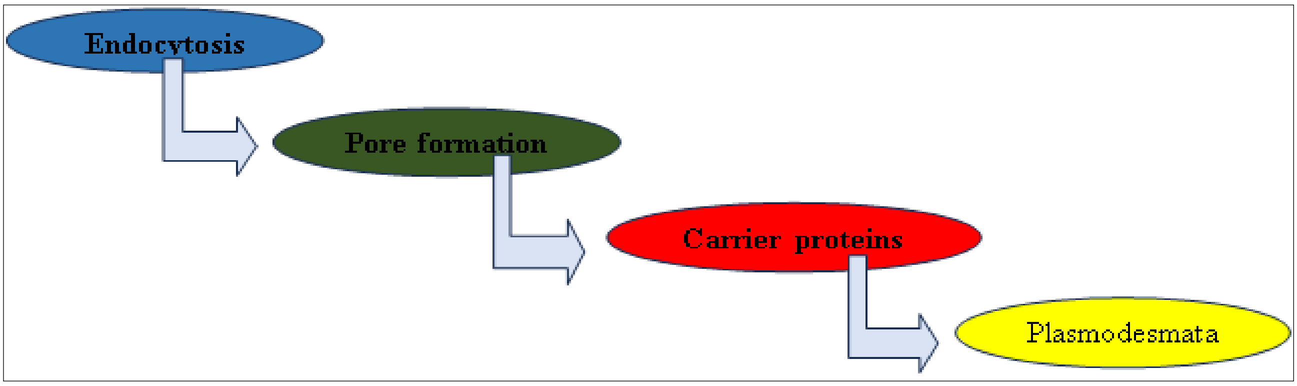

Fig. 1. Movement of nanoparticles.

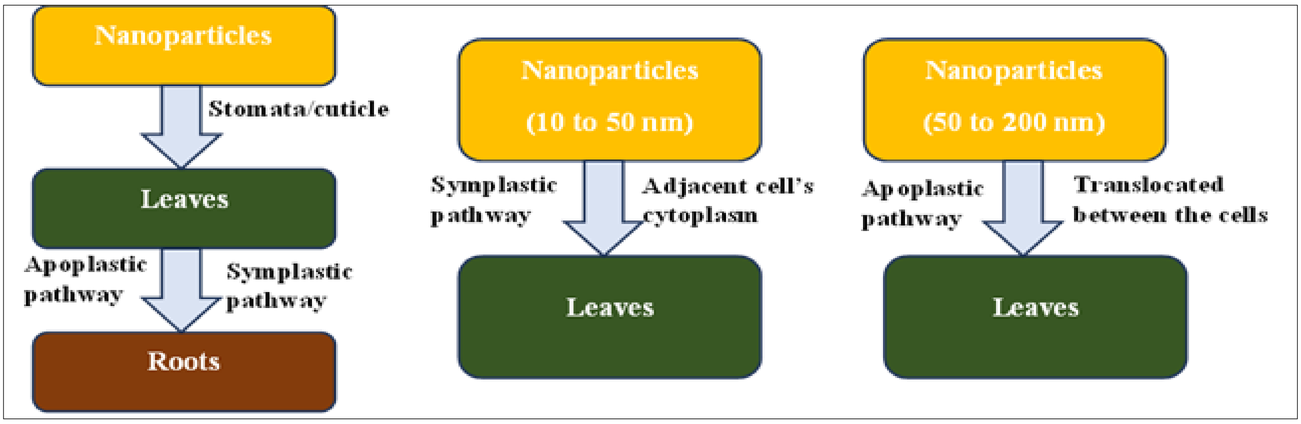

Fig. 2. Movement of nanoparticles from root to leaves.

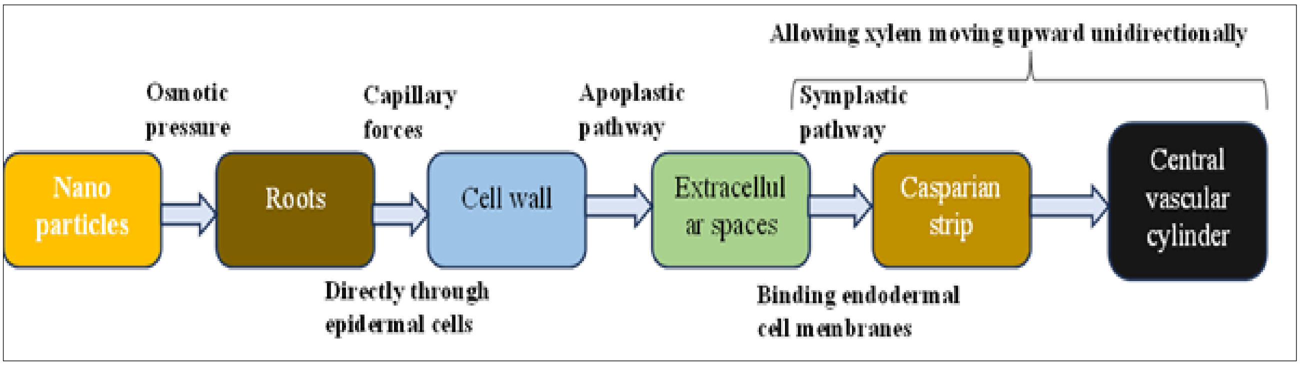

Fig. 3. Movement of nanoparticles from leaves to root.

In addition, seeds can absorb nanoparticles through passive diffusion in the cotyledon or through parenchymatic intercellular spaces in the seed coat, suggesting a potential route for seed priming applications (7).

The stomata or cuticles on the leaves facilitate the entry of nanoparticles that the leaves absorb. The cuticle functions as the primary barrier for macro particles, but it allows entry of nanoparticles smaller than 10nm (16). The apoplastic and symplastic routes facilitate the transfer of particles into the plant's vascular system (15, 17). The cytoplasm of adjacent cells serves as the favoured conduit for the symplastic transfer of nanoparticles ranging from 10 - 50 nm (18). The apoplastic pathway facilitates the movement of larger nanoparticles (ranging from 50 - 200 nm) between cells via the phloem sieve tubes, with ingested nanoparticles transported alongside the sugar flow (16).

Due to the high sap sink properties of roots, stems, fruits, grains and young leaves, phloem vascular transport facilitates the bidirectional movement of nanoparticles, resulting in their accumulation in various organs to varying extents (15). The phrase "nonselective direction of least resistance" pertains to apoplastic transport. The apoplastic channel for translocation is often regarded as the optimal route for numerous water-soluble nutrients and superfluous metal complexes. The principal variables influencing the effective adsorption of nanoparticles after foliar application were size, concentration, climate and application methods (7). The chemical composition and morphology of the leaf, the existence of trichomes and the occurrence of waxes and exudates on the leaf surface are all critical factors that affect the retention of nanoparticles (19).

Accumulation of various nanoparticles in different crop tissues

The accumulation of nanoparticles in various plant tissues varies significantly depending on the crop species, nanoparticle type and concentration applied, as illustrated in Fig. 4. For silver nanoparticles (AgNPs), *Glycine max* (soybean) exhibited beneficial effects on both root (2102 mg kg^{-1}; helps in increase the number of root nodules and the length of the roots) and shoot (1135 mg kg^{-1}; helps in increase in number of primary and secondary branches) at a concentration of 4000 mg L^{-1}. On the other hand, at a concentration of 1000 mg L^{-1}, the rice crop demonstrated 5 mg kg^{-1} accumulation in the shoot, while the root was 1544.1 mg kg^{-1}. In *Solanum lycopersicum*, a lower concentration of 450 mg L^{-1}resulted in no root accumulation, but a shoot accumulation of 50 mg kg^{-1} was noted.

Copper nanoparticles (CuNPs) were administered at varying concentrations to different crops, namely *O. sativa*, where a concentration of 1000 mg L^{-1} resulted in a larger accumulation in the roots, reported at 1544.1 mg kg^{-1}, compared to the shoots, which was 17.27 mg kg^{-1}. No accumulation was observed in the shoots of *Brassica juncea* at a concentration of 1500 mg L^{-1}; however, a concentration of 190.4 mg kg^{-1} was detected in the roots. Concentrations below 500 mg L^{-1} were administered to *Cajanus cajan* (20 mg L^{-1}), *Vigna radiata* (125 mg L^{-1}), *Lactuca sativa* (250 mg L^{-1}) and *Phaseolus vulgaris* (100 mg L^{-1}), resulting in satisfactory root accumulation levels (*O. sativa* - 5.82 mg kg^{-1}; *L. sativa* - 3773 mg kg^{-1}; *P. vulgaris* - 800 mg kg^{-1}), except for *V. radiata*. In terms of shoot accumulation, only *O. sativa* (19.06 mg kg^{-1}) and *V. radiata* (18.46 mg kg^{-1}) exhibited any accumulation, while the other two species did not show any measurable accumulation.

In case zinc nanoparticles (ZnNPs) were administered to *S. lycopersicum* at a concentration of 1000 mg L^{-1}, resulting in a shoot accumulation of 250 mg kg^{-1}. In *Zea mays*, a concentration of 100 mg L^{-1}led to a root accumulation of 10 mg kg^{-1} and a shoot accumulation of 30 mg kg^{-1}.

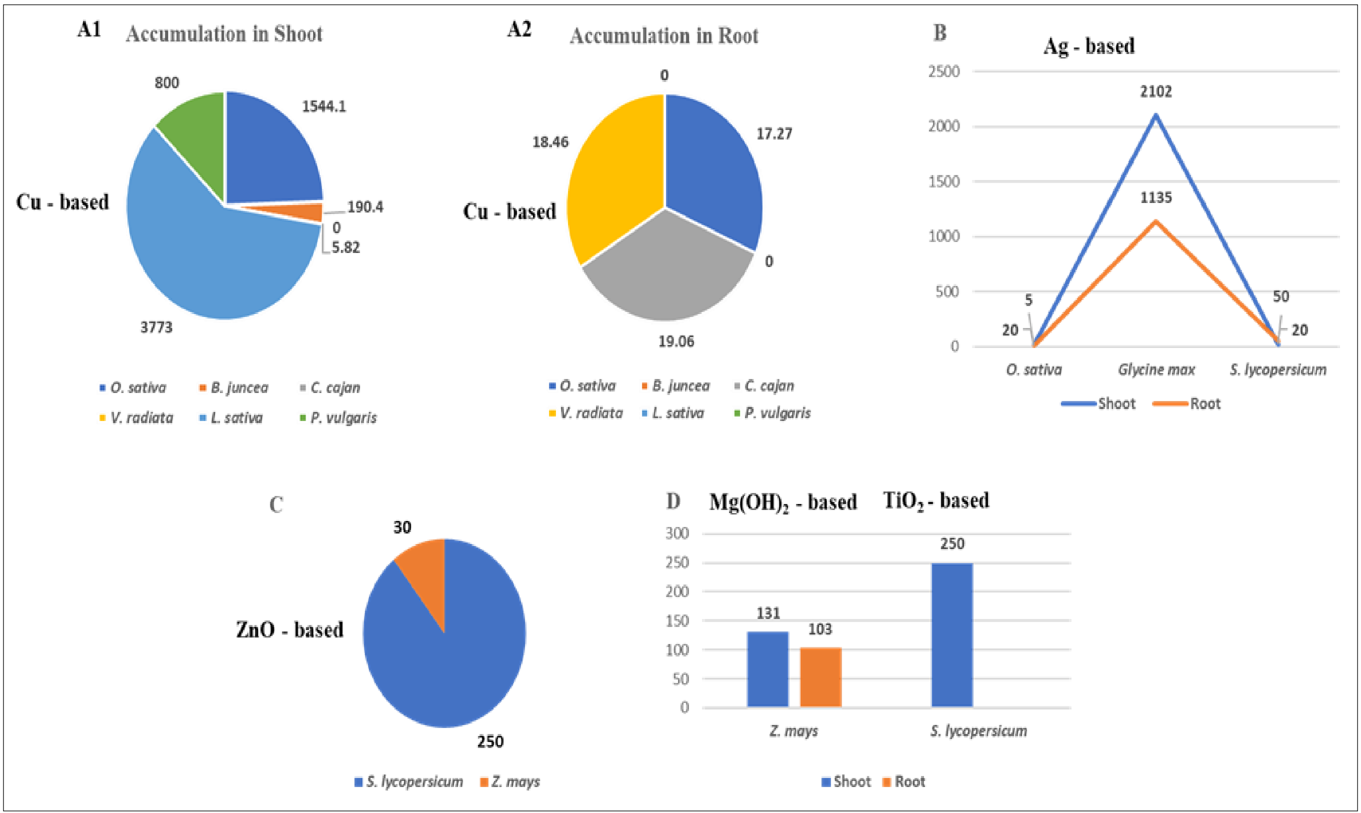

Fig. 4. Accumulation of different nanoparticles on shoot and roots of various crops (mg kg^{-1}).

Magnesium hydroxide [$Mg(OH)_2$] and titanium dioxide (TiO_2) were administered at an identical dose of 1000 mg L^{-1} across two distinct crops. *Z. mays* exhibited an accumulation of 103 mg kg^{-1} in roots and 131 mg kg^{-1} in shoots, while *S. lycopersicum* demonstrated a 250 mg kg^{-1} accumulation solely in shoots, with no accumulation in roots.

Translocation mechanism of nanoparticles in plants

Understanding the mechanisms of nanoparticle absorption, translocation and storage within plants requires an integrative view of plant cell physiology, soil interactions and the physicochemical properties of nanomaterials (20, 21). Plant cell walls serve as a specific barrier that regulates the ingress of nanoparticles into the cell and determines their ability to dissolve and permeate the cell based on their properties (22). Most research indicates that the primary obstacle hindering nanoparticles from penetrating plant cells is the size of the pores in the cell wall (7). Nanoparticles must measure 40–50 nm to penetrate the cell from the plant's surface. A secondary restriction influencing the capacity of nanoparticles to traverse the cell wall and membrane or to promote adherence to the radical surface or exudates, is their composition (7). Beyond size, nanoparticle composition and surface properties-such as positive charge, morphology and surface coating strongly influence their adhesion to root surfaces, uptake efficiency and movement within the plant (24, 25). Positively charged nanoparticles tend to bind more readily to the negatively charged plant cell walls, enhancing cellular entry. Additionally, interactions in the rhizosphere, including binding with root exudates or soil colloids, can modulate nanoparticle behaviour and bioavailability. The stability and persistence of nanoparticles in the soil further dictate their potential to be absorbed and translocated within plant tissues (23).

Plant-nanoparticle interaction mechanisms

Impact of nanoparticles on plants

Roots and leaves function as the primary entry points for nanoparticles into the plant system (16). Upon entering plants, nanoparticles interact with them at the cellular and subcellular levels, leading to morphological (disorganisation of thylakoid membranes and swelling of entire organelle) and physiological changes (disruption of the electron transport chain, decrease in photosynthetic efficiency and reduction in energy production). The interactions might be either advantageous (ZnO or CuO nanoparticles act as an essential source of micronutrients) or harmful (Ag or CdTe nanoparticles are highly toxic to plant cells even at low concentrations), depending on the plant species and the particular nanoparticles involved (27). The influence of nanoparticles on plant systems may be contingent upon their dimensions, chemical composition, reactivity and concentration within or on the plant (16). The researchers utilised various nanoparticle application methods, including soil application, foliar spray and seed treatment, to examine the impact of nanoparticles on seed germination and plant growth (1). Current evidence suggests that, at concentrations below certain limits, many nanoparticles can enhance seed germination and promote plant growth and development. The bulk of these studies were performed in controlled treatment settings, including hydroponic conditions, pot environments and plate growth mediums, to understand the advantageous effects of nanoparticles on plant growth and seed germination, as well as their role in augmenting plant resilience to stress (2).

Seed germination

Seed germination is the fundamental process for plant growth, development and production (28). The output from a natural germination process is rather low and requires considerable time. Nanoparticle treatments, particularly via seed coating or priming, have shown promise in enhancing water uptake and germination speed. Numerous experiments have been undertaken to assess the ability of nanoparticles to enhance germination. The precise method by which nanoparticle treatments enhance seed germination rates remains unidentified (29). Nanoparticle treatments may enhance seed germination by augmenting seed uptake and water retention. Following a two-day incubation period, the moisture content of tomato seeds treated with carbon nanotubes (CNTs) was 19 % higher than that of the untreated seeds (13). The results indicated that the CNTs enhance water absorption and retention (16). The precise mechanism remains unidentified; nevertheless, it is conceivable that the CNTs generate micropores and channels facilitating water infiltration into the seed coverings. One hypothesis is that CNTs may influence the expression or function of aquaporins (AQPs), membrane-bound proteins that regulate water transport within cells (30, 31). This interaction could potentially accelerate seed imbibition, leading to faster and more synchronised germination.

Beneficial impact of nanoparticles on growth and yield

Table 1 illustrates the beneficial effects of various nanoparticles on crop plants, including increases in metabolite content, increased fruit yield, shoot and root elongation, seed germination and vegetative biomass (32). Crops such as peanuts, soybeans and spinach exhibit substantial alterations in several biochemical parameters (photosynthetic pigments: Chl a, b and total carotenoids; enzyme activity, nitrogen metabolism enzymes: nitrate reductase, nitrite reductase, glutamine synthetase) related to plant growth and development by improving nitrogen utilisation efficiency and photosynthetic rate (1). Nanoparticles can enhance plants' resistance to abiotic stressors and diseases, as well as improve nutrient uptake. Nanoparticles can influence plant growth and development by altering certain physiological processes (16). Investigations into plant toxicity evaluated the influence of nanoparticles on biomass accumulation and germination rates, with most studies indicating that they can exert detrimental effects at certain dosages. Certain research indicates that nanoparticles may substantially affect plants (5).

In *B. juncea* and *P. mungo*, carbon nanotubes demonstrated 100 % germination across all concentrations (1). The root length and number of root hairs rise dramatically at a concentration of 20 ppm, while there is a modest decline in the number of root hairs at a higher dose of 40 ppm (1). Optimal concentrations of ZnNPx in mung bean and chickpea demonstrate beneficial effects on seed germination, seedling growth rate and root and shoot development; however, negative effects were noted when concentrations surpassed a certain threshold (34). FeO nanoparticles at 100 ppm enhance seedling growth, whereas greater concentrations of the same nanoparticles impede seed germination, lower the germination rate and diminish root biomass in wheat crops (35). Elevated concentrations of TiO_2 nanoparticles exhibit neutral effects, TiO_2 bulk demonstrates inhibitory effects, while low quantities (2 and 10 ppm) of TiO_2 nanoparticles have been shown to enhance shoot lengths in wheat seedlings (47). The application of silica nanoparticles at a rate of 15 kg ha^{-1} to maize crops significantly enhances various growth parameters, including the number of shoots and roots, stem height, stem diameter, leaf area and root length, with no adverse effects observed at 20 kg ha^{-1} (36).

Plant stress tolerance and the function of nanoparticles

Plants can adapt to or endure adverse conditions such as heat stress, salinity, cold and drought (6). A multitude of cellular and molecular investigations have been performed on plants' responses to abiotic stress (37). Abscisic acid, reactive oxygen species (ROS), cytoplasmic calcium ions (Ca^{2+}) and activated mitogen-activated protein kinase (MAPK) pathways are the primary responses of plants to abiotic stimuli (1). During the advanced phase of the stress response, stress-specific genes are activated and proteins that safeguard cells from damage are regulated (38). Increasingly**,** nanoparticles are being investigated for their role in modulating these stress responses and enhancing plant tolerance under harsh conditions.

Nanoparticle bioavailability modulated by rhizosphere processes

The food plant and quality could be improved by nanoparticles at surprisingly modest quantities. The bioavailability and mobility of nanoparticles may decrease in soil due to its large reactive surface, where the nanoparticles aggregation takes place, thus hindering the growth, quality and yield of food plants (39). To address this, strategies such as modifying nanoparticle surfaces, using rhizosphere-targeted fertilisers or employing direct application methods like foliar sprays or root zone emulsions have been proposed to improve their bioavailability and functional delivery to plants (40).

Biological responses of nanoparticles in plants

The speed in production of phytohormones, primary and secondary metabolic pathways, differential expression of genes for elemental transporters and the activity of antioxidant enzymes in plants may increase after several rhizosphere events (42). Not only the absorption and transport of plant nutrients, but also the biochemical and metabolic pathways of nutritional quality (synthesis of amino acids, carbohydrates and fatty acids) have been regulated by nanoparticles (43). For example, the application of ZnO and CuO nanoparticles in *Glycyrrhiza glabra* (liquorice) seedlings significantly increased the accumulation of

Table 1. Positive responses of nanoparticles on plant growth

Nanoparticles	Concentrations	Size (nm)	Effects on Plants	Crops
Activated carbon-based TiO_2	0-500 mg L^{-1}	30-50	Enhanced germination	*Solanum lycopersicum L.*
CuO	500 mg kg^{-1} sand culture		Rise in biomass	*T. aestivum*
TiO_2	0.01-0.05 %	4-6	Growth acceleration, elevated glutamate dehydrogenase and glutamic pyruvic transaminase activity	*Spinacia oleracea*
SiO_2	5mM	4-10	Rise in shoot biomass and grain weight	*O. sativa*
TiO_2	300-1000 mg L^{-1}	30	Hydraulic conductivity inhibition	*Z. mays*
MWCNT	49 mg mL^{-1}		Nutrient uptake (Fe, Mn, Zn, K and Ca)	*L. esculentum*
SWCNT	325-1750 mg L^{-1}	8	Rise in root length	*Allium cepa* and *Cucumis sativus*
ZnO	20 ppm foliar spray	1.2-6.8	Rise in biomass	*Vigna radiata*
TiO_2	1000 mg L^{-1}		Chlorophyll content	*T.aestivum*

antioxidant compounds such as flavonoids, anthocyanins and phenols (44). Subsequent exposure to graphene oxide metabolic pathway of phenylalanine in rice crop was up-regulated (45).

Limitations of nanoparticles

Nanoparticles' small size and enormous surface area make them extremely reactive (7). Another issue with these materials is their reactivity and unpredictability. Farm workers may be exposed to xenobiotics during their application, which presents safety issues (46). This includes those involved in both the manufacturing of nanofertilizers and their application in the field. Not withstanding the anticipated benefits, it is imperative to assess the feasibility and significance of these innovative smart fertilisers. Indeed, their popularity in sustainable agriculture is limited by significant concerns regarding their transport, toxicity and bioavailability, as well as potential unexpected environmental effects upon exposure to biological systems (7). Establishing objectives for toxicological research, alongside risk assessment and hazard identification of nanoparticles, including the evaluation of nanomaterial or fertiliser life cycles, is essential. This is especially true in light of the buildup of nanoparticles in plants and possible health risks (16). In fact, there are now major worries about food safety, human health and food security due to the use of nanofertilizers made from nanoparticles (7).

Studies have documented the phytotoxic effect of nanoparticles and the type, species, dose and application method all affect how well the nanoparticles are absorbed, translocated, transformed and accumulated in plants (composition, size, shape, surface properties) (47). Assessing the toxicity levels of individual nanoparticles in specific crops is crucial for comprehending their uptake and translocation, potential transformations upon interaction with soil and plant compounds and accumulation within various plant tissues (7).

Conclusion

The formation of nanoparticles has been proposed by nanotechnology research in recent years as a potent method to address current challenges associated with conventional fertilisers in traditional agricultural systems. There is strong scientific evidence that nutritional elements containing nanoparticles (such as Fe, Cu, Se and Co) are effective in enhancing the micronutrients of plants. This is evidenced by enhanced growth metrics and significant physiological advancements, including chlorophyll and carotenoid levels, metabolic pathways, photosynthetic efficiency and transpiration rates. The accurate dosage and effectiveness of nanoparticles on plant surfaces provide significant challenges; therefore, minimising the leakage of chemical products from bulk materials, such as mineral fertilisers, has become a priority advantageous characteristic that enables the prospective utilisation of nanoparticles. To figure out the function of nanoparticles within and outside of plants and their environmental impacts, a meticulous study conducted in controlled settings is desperately required. Building an application strategy requires a consciousness of the essential dosage of nanoparticles, length of exposure, translocation and accumulation processes and the mechanism of action on plants. Further determining the precise consequences of nanoparticles and their effects on the ecosystem is crucial.

Acknowledgements

All the authors gratefully acknowledge their parent institute for its unwavering support and technical assistance in fulfilling this review.

Authors' contributions

DH, RS, TL and TP conceived and designed the review, carried out the concept, prepared the figure. KZ and RH provided guidance on the whole concept and improved the manuscript. TRB read and approved the final version of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare they do not have any conflict of interest.

Ethical issues: None

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Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

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