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REVIEW ARTICLE

Tracking nanonutrients in plants: A review of uptake, assimilation, translocation and analytical techniques

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Abstract

The development of nanotechnology in agriculture has fuelled the rise of nanonutrients as prospective agents to improve nutrient use efficiency, crop yield and environmental sustainability. In contrast to traditional fertilisers, nanonutrients offer targeted delivery, slow release and enhanced absorption due to their nanoscale size and distinctive physicochemical properties. This review critically assesses the existing knowledge on nano-nutrient uptake, assimilation and translocation in plant systems. It emphasises the intricate interactions between plant physiological pathways and nanomaterials, including entry modes through leaves and roots, transport mechanisms at the cellular level and their ultimate distribution within plant organs. Additionally, this article provides a detailed account of the methodological strategies employed to investigate these processes. These methods include elemental and isotopic tracing, spectroscopic and molecular analyses, imaging technologies, physiological and biochemical assays, as well as dye-based tracking systems. The combination of these methodologies has enhanced our ability to quantify, visualise and comprehend the fate of nanonutrients in plants. Synthesising recent breakthroughs and methodological updates, this review aims to establish a foundation for future studies that maximise nano-fertiliser design and ensure their safe and efficient deployment in sustainable agriculture.

Keywords: assimilation; detection approaches; nano fertilizer; plant-nanomaterial interaction; translocation; uptake

Introduction

Globally, cultivable land is under immense pressure to meet the growing food demand of a rapidly expanding population, while shrinking cultivable land and the overuse of chemical fertilisers have led to numerous environmental concerns, including land degradation, groundwater contamination and greenhouse gas emissions. The nutrient use efficiency (NUE) of chemical fertilizers remains low, less than 50 % of applied nitrogen is typically absorbed by crops, while the rest is lost (1). In addition to nitrogen, phosphorus and potassium fertilisers also exhibit low recovery rates in plants-often below 20-30 % which leads to nutrient runoff, eutrophication of water bodies and disruption of soil microbial balance. Micronutrient fertilisers, such as iron and zinc, often suffer from fixation in the soil, reducing their availability to crops and requiring repeated applications. These practices not only burden the environment but also increase the input costs for farmers and contribute to unsustainable agricultural intensification (2).

Furthermore, long-term reliance on synthetic fertilizers contributes to soil acidification, loss of organic matter and declining soil fertility. Excessive fertiliser usage, without proper synchronisation with plant demand, has also been associated with reduced nutrient use efficiency and crop quality. To address these concerns, researchers around the world are exploring better and efficient alternatives for them, in this scenario nano fertilizers have emerged as a promising solution (3).

As elemental particles, encapsulated nutrients, or loaded onto polymers or bio-based materials, nano fertilisers deliver nutrients in the form of particles ranging from 1 to 100 nm. Broadly, nano fertilizers can be categorized into: (i), nano-encapsulated nutrient particles like nano-ZnO and nano-Fe; (ii) nutrient-encapsulated lipid or polymer carriers; and (iii) nutrient-loaded chitosan, clay, or carbon-based nano-carriers (4). Nano-scale materials not only yield an enhanced surface area but also heightened reactivity and controlled release, which helps improve uptake efficiency and minimise environmental loss (5). Whether through soil or foliar application, the release of nutrients is gradual, allowing for better interaction with plant tissues, which improves nutrient uptake and helps match the plant's demand throughout its growth stages. Moreover, some of these formulations offered by nanotechnology boost metabolism and thus supports growth while increasing tolerance to stress (6). Regardless of the promise they hold, the actual mechanisms of action of nano fertilizers in plants is still a mystery.

The processes of uptake (entry into roots or leaves), assimilation (incorporation into biochemical pathways) and translocation (movement across plant tissues) are complex systems that also depend on a plant's species, its physiological attributes and even its surface charge (7). Moreover, there are reports of increased biomass and enhanced nutrient accumulation, as well as improved photosynthetic efficiency. For example, zinc oxide nanoparticles have been shown to enhance the uptake of zinc and boost yields for several cereal crops (6). Furthermore, nano-urea formulations have been reported to enhance nitrogen use efficiency in India (4). However, other researchers have raised concerns about sparse or inconsistent responses and suggest that these findings challenge accepted notions of plant physiology, calling for deeper inquiry into the fundamental processes at play (8).

These discrepancies in findings underscore the need to investigate the mechanisms of nano fertilisers further. In several situations, the mechanisms by which nano fertilisers exert their influence on plants are poorly understood. Questions remain surrounding the uptake of nano fertilizers: are they absorbed by plants as particles or ions? Do they bypass plant barriers and affect gene expression, or impact genes involved in vital physiological processes, such as the regulation of enzymes (9)? Moreover, there is the possibility that nanomaterials undergo changes at the soil-plant interface, such as aggregation, dissolution, or interaction with root exudates, complicating their tracking and efficacy assessment (7). To dissect these interactions, one focuses on tracing and characterising nano-nutrients within plant tissues through imaging methods, such as fluorescence imaging, spectroscopic techniques including FTIR and XRD, as well as isotopic labelling with ^{15}N and ^{68}Zn (10). The influence, at both cellular and molecular levels, of nano-nutrient incorporation is also examined through complementary physiological, enzymatic and omics techniques (7).

The novelty and complexity surrounding nano fertilizers in agriculture is what prompted this review. It aims to thoroughly describe the mechanisms of uptake, incorporation into plant biochemistry and transport through the plant system. Uptake, assimilation and translocation are studied through a diverse range of methodologies, from classical nutrient quantification and enzymology to advanced imaging and isotopic techniques. By integrating mechanistic understanding with methodological critique, this article aims to inform ongoing work and facilitate the structured development of scientifically rational and agronomically impactful nano fertilisers.

Nano fertilizers: Types, characteristics and applications in sustainable agriculture

The increasing global population has created a higher demand for food. As such, the agricultural sector is working towards implementing more sustainable practices that are both environmentally friendly and increase crop productivity (5). The use of chemical fertilisers is common in agriculture because it increases yields. However, it has several downsides, such as nutrient losses via leaching, volatilisation and runoff, which lead to soil degradation, water pollution and low nutrient use efficiency (NUE). The application of nanotechnology offers a solution to these problems through the creation of nano fertilisers (NFs), which aim to provide plants with nutrients more efficiently (11).

Classification of nano fertilizers

Nano fertilisers can be categorised according to their composition, structure and nutrient delivery methods (4). nano -scale nutrient particles, such as iron oxide (FeO_3) or zinc oxide (ZnO), are composed of nutrients that have been reduced to nanometric sizes (1-100 nm) (12). Examples of nutrient-loaded nanocarriers include silica nanoparticles, carbon nanotubes and polymeric carriers such as chitosan, which act as nutrient carriers (13). The precise delivery of nutrients to plant tissues is made possible by their attachment to the surface or enclosing within the carrier (14). For example, silica nanoparticles have been used to transport phosphorus and nitrogen, increasing nutrient uptake and reducing losses (15). To facilitate controlled release, nutrients in encapsulated or coated nanoformulations are either encapsulated within or coated by nanomaterials, such as biopolymer layers, clay-based matrices, or polymer films. One excellent example is urea coated with hydroxyapatite nanoparticles, which releases nitrogen gradually over 40-50 days much longer than the 4-10 days that conventional fertilisers typically release (16).

Key physicochemical properties of nanomaterials affecting uptake, assimilation and translocation

The effectiveness of NFs in agriculture depends heavily on their physicochemical properties, which determine how they interact with plants and their surrounding environment (17).

Size and surface area

NFs have a high surface area-to-volume ratio due to their nanoscale dimensions (1-100 nm), which boosts their reactivity and capacity to enter plant tissues (18). Because they can more readily pass through plant cell walls, which normally have pores of 5-20 nm, via pathways like endocytosis or ion channels, smaller particles-such as 20 nm ZnO nanoparticles-show better NUE than larger ones (e.g., 50 nm) (19). Additionally, this facilitates foliar uptake, in which nanoparticles interact with carrier proteins or enter through stomata (20).

Shape and crystallinity

The way that nanoparticles move through plant tissues and interact with plant surfaces depends on their shape, whether it is spherical, rod-like, or tubular (21). Compared to rod-shaped nanoparticles, which are more likely to clump, spherical ones typically offer better dispersion and uptake (22). Solubility is influenced by crystallinity; amorphous nanoparticles dissolve more easily than crystalline ones, which affects the rates at which nutrients are released (23). Amorphous silica nanoparticles have been found to offer a more reliable nutrient release, supporting steady plant growth (24).

Surface charge and agglomeration

The stability and ability of NFs to interact with plant cells, which typically have a negatively charged surface, are influenced by their surface charge, which is often modified with coatings such as chitosan (25). Positively charged nanoparticles, such as those coated with chitosan, exhibit better adherence to plant tissues, thereby improving the delivery of nutrients (26). Agglomeration, however, can reduce penetration and increase particle size, potentially compromising efficacy (27). By encapsulating nanoparticles in natural substances like flavonoids, biological synthesis techniques, such as plant extracts, help prevent agglomeration and enhance dispersion and absorption (28).

Common nano-nutrients used in agriculture

To address specific deficiencies and promote plant development, nano fertilisers contain essential macro- and micronutrients (29). ZnO nanoparticles are frequently used to address zinc deficiencies, a problem that affects more than 50 % of agricultural soils worldwide. In crops such as maize and onions, they enhance root development, seed germination and chlorophyll production, thereby increasing yield and nutritional quality (30, 31). However, iron deficiency in crops like soybeans can be addressed with the help of FeO_3 nanoparticles, which are an efficient iron source (32). They improve photosynthesis and overall plant health; field tests have shown that applying nano-Fe-coated urea can increase wheat yield by up to 8.3% while reducing nitrogen losses by 24% (1). Nano-urea formulations that minimise leaching and volatilisation by providing a slow-release mechanism for nitrogen include urea-hydroxyapatite nanohybrids (33, 34). When compared to conventional urea, these NFs have increased rice crop yields by up to 20 % (35). As sources of micronutrients, CuO and MnO nanoparticles support plant enzymatic activity and stress tolerance (33). For instance, it has been demonstrated that Mn nanoparticles increase the photosynthetic efficiency of mung beans, while CuO nanoparticles improve disease resistance in tomatoes (15).

Recent applications and field-level results

Field-level trials serve as a critical validation step for nano fertilizers beyond controlled conditions. Several large-scale studies have confirmed the agronomic efficacy of nano formulations across a variety of crops and geographies. For instance, multi-location trials conducted by IFFCO in India using nano urea have demonstrated that 50 % of conventional urea can be replaced without yield penalties in crops such as rice, maize and wheat, leading to both cost savings and reduced nitrogen losses through volatilisation and leaching (36). In maize, foliar nano-urea applications resulted in 15-18 % higher grain yield, an improved SPAD chlorophyll index and better root-to-shoot nitrogen translocation compared with conventional urea (37). In wheat, ZnO nanoparticles increased grain zinc content by up to 30 %, directly addressing human micronutrient deficiency (hidden hunger). Similarly, nano-Fe-coated urea was reported to enhance wheat yield by 8.3 % while reducing nitrogen loss by 24 % compared to traditional practices (38). In another study on fig orchards, the application of bio-nanofertilizers, which combine beneficial microorganisms and nano-formulated nutrients, improved soil microbial activity and increased nutrient cycling, indicating synergistic effects (39).

Moreover, climate-resilient applications have been reported. For example, foliar-applied silica nanoparticles in barley helped mitigate salinity stress by enhancing K^+ uptake and reducing Na^+ accumulation, improving seedling growth by 25 %. These real-world outcomes not only validate the physiological and biochemical benefits observed under laboratory conditions but also highlight the potential of nano-nutrients in sustainable and climate-smart agriculture. However, field performance can vary across soil types, environmental conditions and application protocols. Standardization of formulation, dose and delivery method is essential before large-scale adoption. Despite these variations, field studies have consistently demonstrated the dual benefits of productivity and environmental safety, making nano fertilizers a promising innovation for future-ready farming.

Potential risks, concerns and adverse effects of metal-based nano fertilizers

Despite their promising benefits, metal-based nano fertilizers pose several ecological and physiological risks that must be critically evaluated. The high surface reactivity, small size and prolonged persistence of metal oxide nanoparticles (e.g., ZnO, CuO, Fe_3O_4) can lead to phytotoxic effects at elevated concentrations or under prolonged exposure. For instance, the excessive application of ZnO nanoparticles has been linked to chlorophyll degradation, membrane damage, oxidative stress and growth inhibition in crops such as wheat and tomato (23). Similarly, CuO nanoparticles may interfere with photosynthetic enzymes and disrupt electron transport chains in plant chloroplasts, potentially causing reduced photosynthetic efficiency (10).

From an environmental standpoint, metal-based nanoparticles that accumulate in soil may alter microbial community structure, affecting nutrient cycling and soil fertility. For example, CuO and Ag nanoparticles have been shown to suppress beneficial rhizobacteria and nitrifying microbes, leading to unintended shifts in rhizosphere dynamics(40). Moreover, the potential for bioaccumulation through the food chain, especially in leafy vegetables or grains consumed directly, raises concerns about human and animal health.

Another key concern is the lack of degradation or transformation mechanisms for many engineered nanoparticles in natural environments. Unlike organic fertilizers, metal-based nanoparticles may persist in soil or water systems, leading to long-term ecological accumulation. Factors such as particle dose, size, coating and environmental pH have a significant influence on nanoparticle fate and toxicity (38). Therefore, while nano fertilizers are heralded as innovative alternatives to conventional inputs, their deployment must be carefully calibrated. Toxicological thresholds, environmental fate and regulatory standards need urgent attention before wide-scale adoption. Future formulations should prioritise biodegradable carriers, green synthesis and ecological risk assessments to mitigate unintended consequences (8).

Uptake mechanisms of nano nutrients in plants: Soil and foliar pathways

Root uptake

The apoplastic and symplastic pathways are the two primary mechanisms by which roots absorb micronutrients (41). Diffusion and mass flow play a major role in the apoplastic path, which involves NPs moving through the extracellular spaces of the root cell walls without passing through the plasma membrane. Smaller NPs (<20 nm) that can pass through the cell wall's porous structure-which has typically pores that range in size from 5 to 20 nm-benefit significantly from this pathway. The Casparian strip in the endodermis, which functions as a barrier and restricts the apoplastic pathway, forces NPs to switch to the symplastic pathway to be transported further into the vascular system. In contrast, the symplastic pathway involves NPs entering the root cell's cytoplasm, often through ion channels or endocytosis and then moving from cell to cell via plasmodesmata, which have a size exclusion limit of approximately 40-50 nm. NPs can move to shoots and leaves through the xylem thanks to this pathway, which permits more regulated and selective uptake (42). In contrast to bulk Zn sources, a study demonstrated that 15 nm ZnO nanoparticles were primarily absorbed through the symplastic pathway in maize roots, resulting in an increase in zinc content in the shoots. Similarly, tomato (*Solanum lycopersicum*) and wheat (*Triticum aestivum*) have shown improved root zinc uptake and increased biomass when treated with ZnO and FeO_3 nanoparticles, respectively, highlighting species-specific responses to nanonutrient exposure. These studies highlights the effectiveness of this route for nanonutrient delivery (7). Fig. 1 explains clearly the foliar and root uptake in plants.

Foliar uptake

Foliar uptake provides an alternative pathway for NP absorption, which is particularly beneficial for addressing micronutrient deficiencies quickly (43). Cuticle penetration and stomatal entry are the primary mechanisms by which this process occurs. Although NPs smaller than 5 nm or those with hydrophilic coatings can pass through lipophilic pathways or aqueous pores within the cuticle, the hydrophobic nature of the cuticle -a waxy layer on the leaf surface -presents a significant barrier to NP entry. However, during times of high transpiration, larger NPs (10-50 nm) can enter through the stomatal aperture, which is usually 10-100 μm wide, making stomatal entry more effective. After entering, NPs can either diffuse into the leaf mesophyll's apoplast or be internalised by cells through endocytosis (44). Research indicates that foliar application of 20 nm Fe_2O_3 NPs on soybean leaves resulted in a 30 % increase in iron content in leaf tissues within 48 hours, primarily through stomatal entry (45), underscoring the potential of this pathway for rapid nutrient delivery.

Aquaporins in NP uptake

Along with other elements like ion channels and carrier proteins, aquaporins-a family of membrane proteins that help move water and small solutes-are important for NP uptake (46). It has been demonstrated that aquaporins, especially those belonging to the plasma membrane intrinsic protein (PIP) subfamily, function as conduits across the plasma membrane to carry NPs smaller than 2-3 nm, like silica NPs. In addition to aquaporins, ion channels and carrier proteins-such as those for phosphate or nitrate-can help absorb nutrient-loaded NPs by identifying the ionic forms released from them (47). By changing their stability and interaction with root surfaces, environmental factors such as soil pH and ionic strength also affect NP uptake. Silica nanoparticles were transported by aquaporins in rice roots at neutral pH levels, thereby increasing silicon uptake and enhancing plant resistance to salinity stress (48). Particle size, surface charge and coatings are among the variables that influence the absorption of nanonutrients. Because they can more easily pass through cell walls and membranes, smaller NPs (e.g., <20 nm) exhibit higher uptake rates, whereas larger particles (>50 nm) tend to aggregate and decrease their bioavailability (49). Another critical factor is surface charge; positively charged NPs, like ZnO NPs coated with chitosan, adhere better to negatively charged plant cell surfaces, increasing uptake efficiency (50).

Root exudates and transporters

The rhizosphere's uptake and bioavailability of nanonutrients are further regulated by root exudates and transporters. By modifying pH, chelating NPs, or encouraging their dissolution, root exudates containing organic acids (like citric acid), sugars and amino acids can change the soil microenvironment and increase nutrient availability. For example, it has been demonstrated that the citric acid released by maize roots increases the solubility of FeO_3 NPs, thereby promoting iron

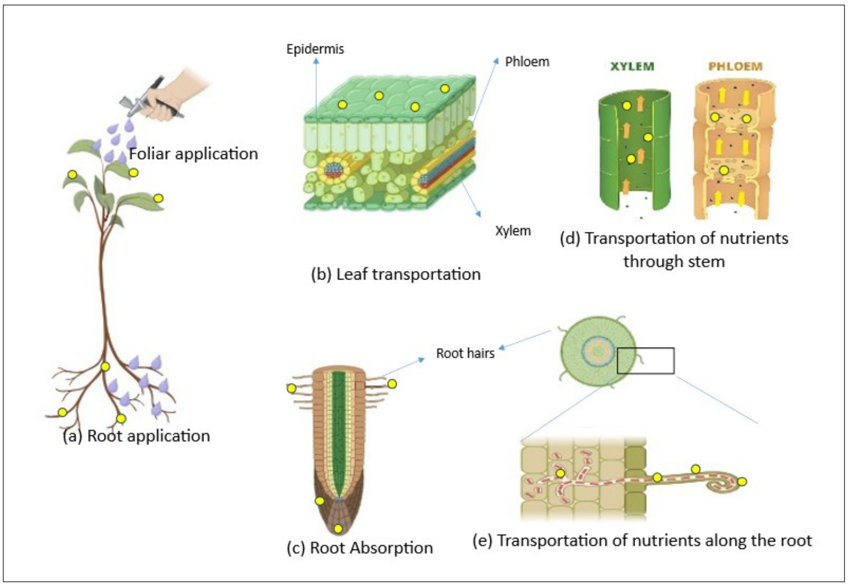

Fig. 1. Schematic diagram explaining the nanoparticles uptake and translocation (a) Root and foliar application of nano nutrients (b) Absorption of NPs through stomata and their entry into the xylem and phloem (c) Absorption of NPs by root hairs (d) Transport of nutrients through xylem and phloem (e) transport of nutrients through root system *via* symplastic or apoplastic pathway.

uptake (51). The active uptake of nutrients released from NPs is crucial for their assimilation into plant metabolic pathways. Examples of these transporters are NRT (Nitrate Transporter) for nitrogen and ZIP (Zinc/Iron-regulated Transporter-like Proteins) for zinc and iron.

In addition to root-mediated processes, the role of plant-associated microbial communities, particularly plant growth-promoting rhizobacteria (PGPR), is crucial in modulating the fate of nanomaterials. PGPR such as *Azospirillum, Pseudomonas and Bacillus species* can enhance nanonutrient availability by producing siderophores, organic acids and biosurfactants that solubilize or chelate nanoparticle-bound nutrients. Moreover, these microbes can form biofilms on root surfaces, facilitating localized NP transformation and enhancing nutrient exchange (52).

Certain microbes may even detoxify potentially reactive nanomaterials, reducing phytotoxicity while synergistically supporting plant growth. For instance, PGPR-mediated biotransformation of ZnO nanoparticles has been demonstrated to enhance zinc uptake efficiency and stimulate the expression of antioxidant enzymes in crops. Such multi-directional interactions highlight the significance of integrated nano-microbe-plant systems for sustainable agriculture. By affecting their transformation and mobility in soil, the rhizosphere microbiome also has a significant impact on NP bioavailability (53). Siderophores that chelate iron from FeO_3 NPs and increase its availability to plants can be produced by beneficial microbes like *Pseudomonas spp*. Similarly, by metabolising coatings or changing their surface characteristics, the phyllosphere microbiome on leaf surfaces can affect NPs applied foliarly. According to a study, tomato plants' rhizosphere microbiome enhanced CuO NPs' bioavailability through microbial-mediated dissolution, improving copper uptake and disease resistance (54). The intricate relationship between NPs and microbial communities is highlighted by the fact that, on occasion, microbial activity can decrease NP bioavailability by encouraging aggregation or changing NPs into less soluble forms.

Assimilation of nano nutrients in plants: Mechanisms and impacts via soil and foliar uptake

Nanonutrients possess unique properties that enable them to enter plant systems through both foliar and soil pathways, allowing for their subsequent assimilation (55). In contrast to traditional fertilisers, NFs provide nutrients in a regulated manner, reducing losses and ensuring that availability meets plant metabolic needs. Optimising their agricultural applications requires an understanding of the assimilation processes of nanonutrients, including their conversion into forms that are metabolically usable, interactions with metabolic and enzymatic pathways, influence on nutrient sensing and signalling, effects on primary and secondary metabolism and specific assimilation pathways, such as nitrate/nano-urea into amino acids.

To support plant growth and development, nanonutrients must be transformed into metabolically usable forms after being absorbed through foliar uptake (through cuticle penetration or stomatal entry) or soil uptake (through apoplastic and symplastic pathways in roots). Depending on the pH and chelating agent levels, nanonutrients such as ZnO or FeO_3 nanoparticles (NPs) can either enter plants as whole particles or dissolve into ionic forms (e.g., Zn^{2+} or Fe^{3+}) in the apoplast or cytoplasm of the plant (56). For example, ZnO NPs dissolve in the leaf apoplast or rhizosphere, releasing Zn^{2+} ions that are then taken up by ZIP (Zinc/Iron-regulated Transporter-like Proteins) transporters and transported into cells (57). The mechanisms and advantages of applying urea fertiliser coated with ZnO nanoparticles (NP) in wheat cultivation were recently illustrated by a study. Zinc and nitrogen were released gradually and continuously when urea coated with ZnO NPs was applied to wheat plants in this study. According to molecular research on zinc uptake pathways, ZnO NPs dissolved in the rhizosphere release Zn^{2+} ions, which are subsequently absorbed by plant roots most likely through ZIP transporter proteins. Concurrently, the nano-urea released urea molecules, which were hydrolysed by soil urease enzymes to produce ammonium (NH_4^+) for plant uptake (58). Due to better nutrient utilisation, the combined application increased wheat yield by 34 % compared to conventional urea. Additionally, the study found that ZnO NP-coated urea enhanced nitrogen and zinc uptake in plants, confirming the notion that nanofertilizers can deliver nutrients more efficiently and precisely. Plant enzymes and chelators, such as organic acids (like citrate) released by roots, frequently aid in this conversion by improving the solubility and bioavailability of nanonutrients and guaranteeing their incorporation into metabolic processes. Key biochemical processes are influenced by the substantial interactions that nanonutrient assimilation has with plant metabolic and enzymatic pathways (30).

Iron, which is a cofactor for enzymes involved in photosynthesis (like ferredoxin) and respiration (like cytochrome c oxidase), is supplied by nanonutrients such as FeO_3 NPs. These NPs improve photosynthetic efficiency and energy production by increasing the activity of these enzymes through a consistent supply of iron (59). Comparably, nano-urea promotes nitrogen assimilation by enhancing the activity of enzymes that convert nitrate (NO_3^-) or ammonium into amino acids, such as glutamate and glutamine, including nitrate reductase (NR) and glutamine synthetase (GS) (60). Because nanonutrients frequently cause a more controlled release than bulk fertilisers, avoiding toxicity from abrupt nutrient spikes, these interactions can result in upregulated gene expression of enzymes involved in nutrient metabolism. In contrast to expectations, foliar application of nano-urea in combination with reduced soil-applied nitrogen (50 % of the recommended dose) decreased the activity of glutamine synthetase (GS) in rice leaves by 28.6 % compared to conventional urea at full nitrogen rates. This study also showed that foliar application of nano-urea lowered grain protein content and yield (61). These findings highlight a critical insight: while nano urea improves nitrogen delivery and may reduce environmental losses, it does not inherently ensure enhanced nitrogen assimilation or grain quality. This emphasises the need for integrated application strategies, where nano-fertilisers supplement but do not fully replace conventional sources, especially in crops sensitive to nitrogen metabolism and protein accumulation. Nevertheless, other research on the foliar application of zinc oxide (ZnO) nanoparticles in rice under stress conditions has demonstrated that nanonutrients can dramatically increase the activity of antioxidant enzymes like peroxidase (POD), catalase (CAT) and superoxide dismutase (SOD), reducing oxidative damage and enhancing plant growth and stress tolerance (62). For instance, applying foliar ZnO NP under chilling stress enhanced SOD activity and upregulated genes that encode antioxidant enzymes, protecting rice seedlings from ROS and enhancing their physiological function (63).

The biosynthesis of substances like phenolics, flavonoids and alkaloids-all essential for plant defence and stress tolerance-is influenced by nanonutrients in secondary metabolism. According to a recent study on tomato plants, applying zinc oxide nanoparticles (ZnO NPs) topically significantly enhanced the synthesis of phenolic compounds, such as flavonoids, which are important byproducts of the phenylpropanoid pathway and are essential for plant defence against biotic stressors, including infections (64). In particular, tomato leaves treated with ZnO NP had higher levels of total phenolic and flavonoid content, which was associated with increased plant resistance to stress. The upregulation of metabolic pathways that support the plant's defence mechanisms and antioxidant capacity is associated with the increased flavonoid production. ZnO NPs further supported both growth and defence functions by increasing chlorophyll content, improving overall plant growth and lowering stress markers (65). The metabolic integration of nanonutrients is highlighted by particular assimilation pathways, such as the transformation of nitrate or nano-urea into amino acids. The GS-GOGAT cycle allows nano-urea to enter the nitrogen assimilation pathway after it is hydrolysed into ammonium. This cycle provides a nitrogen source for the biosynthesis of amino acids by first allowing GS to incorporate ammonium into glutamine, which is subsequently transformed into glutamate-by-glutamate synthase (GOGAT). After being reduced to nitrite by nitrate reductase (NR) and subsequently to ammonium by nitrite reductase (NiR), nitrate from soil or foliar-applied nano-NPs proceeds in a similar manner.

These amino acids, such as glutamate, play a crucial role in plant growth and development by serving as building blocks for other amino acids, proteins and nucleotides. Regarding its effects on nitrogen assimilation, grain quality and nitrogen use efficiency, field research on the application of nano-urea in rice has produced conflicting findings (66). The majority of recent controlled trials do not support the statement's dramatic increases in amino acid or protein content, despite some research showing that nano-urea can improve input efficiency and reduce the need for conventional urea by up to 25 %, which could result in better growth and possibly higher grain quality. A two-year field study revealed that using nano-urea instead of conventional urea to replace half of the recommended nitrogen dose actually reduced the protein content of grain by 35 % and decreased the activity of important nitrogen assimilation enzymes, such as glutamine synthetase and glutamate synthase (61).

Across multiple species, including maize, soybean, tomato, rice and barley, nanonutrients have demonstrated positive regulation of key physiological and biochemical pathways, such as antioxidant defence, nitrogen assimilation and secondary metabolism. These benefits, however, are strongly dose-dependent. For example, tomato plants treated with ZnO NPs at 25 mg/L exhibited increased flavonoid content and improved stress tolerance; however, higher concentrations (>100 mg/L) resulted in reduced chlorophyll and phytotoxic effects. Similarly, Fe_2O_3 NPs enhanced nodule biomass and shoot growth in soybean at 30 mg/L, while excessive doses reduced nutrient uptake efficiency. These observations underscore the importance of optimising nanoparticle concentration based on plant species and physiological targets, as nanonutrients can exhibit biphasic effects-stimulating at low levels and inhibitory at high levels (67).

Translocation of nano nutrients within plant systems: Mechanisms and dynamics via soil and foliar uptake

Plants absorb nanonutrients through both foliar (leaf) and soil (root) pathways, but their effectiveness depends on their ability to move from uptake sites to various plant tissues, where they are required for metabolic processes. Optimising the use of nanonutrients in sustainable agriculture requires an understanding of their translocation mechanisms, which include their movement from uptake sites to sink tissues, mobility within xylem and phloem, partitioning into roots, shoots, leaves and grains, the temporal dynamics of nutrient redistribution and interactions with transport proteins and chelation processes. To support growth and development, nanonutrients must be transferred from their entry points-either through roots (via soil uptake) or leaves (via foliar uptake)-to sink tissues, such as developing shoots, leaves, flowers, or grains (33).

The apoplastic (extracellular) or symplastic (intracellular) pathways are the primary mechanisms by which roots absorb soil-applied nanonutrients, such as ZnO or Fe_3O_4 nanoparticles (NPs), which pass through the root cortex and endodermis before reaching the vascular system. After entering the xylem, the transpiration stream propels these nutrients upward to the plant's aerial sections. However, foliar-applied nanonutrients must first enter the leaf apoplast or cytoplasm before being redistributed. They enter leaves through stomatal openings or cuticle penetration. Larger particles may dissolve into ionic forms (such as Zn^{2+} or Fe^{3+}) in the apoplast, allowing them to move into the phloem for downward transport to roots or other sinks. In comparison, smaller particles (less than 20 nm) can be internalised by leaf cells via endocytosis (35, 68). Studies on the effective movement of nanonutrients from uptake sites to metabolically active tissues in crops such as maize and soybeans demonstrate that these nutrients support crucial physiological functions.

The effectiveness of root-to-shoot transport mechanisms has been demonstrated by studies employing nanomaterials, such as multiwall carbon nanotubes (MWCNTs), in maize and soybeans. Soybean (*Glycine max*) and cucumber (*Cucumis sativus*) exhibited effective xylem and phloem mobility of CeO_2 and CuO nanoparticles, confirming long-distance translocation and enhanced nutrient redistribution. These studies have demonstrated that nanoparticles are quickly absorbed by roots and transported to shoots via the xylem, with accumulation observed in various plant tissues and cellular compartments within days of exposure (69). However, it has been demonstrated that foliar-applied nano-iron fertilisers in soybeans not only increase photosynthetic rates and yield but also affect root development and nutrient redistribution. This suggests that a sizable amount of absorbed iron can move in both directions, from leaves to roots (70). Enhancing crop growth and productivity by supporting processes such as photosynthesis, grain filling and stress responses, this dynamic transport ensures that vital nutrients delivered as nanoparticles reach sink tissues, including developing grains or roots.

Xylem and phloem mobility of nano nutrients

The ability of nanonutrients to move through the xylem and phloem, which have different functions in nutrient transport, is essential to their mobility within the plant vascular system. Driven by transpiration pull and root pressure, xylem transport is primarily responsible for the upward movement of water and dissolved nutrients from roots to shoots (71). Although intact NPs smaller than the xylem vessel diameter (usually 20-100 nm) can also move directly, nanonutrients absorbed by roots, such as nano-urea or CuO NPs, are frequently transported as ionic forms after dissolving in the root apoplast or cytoplasm. The unidirectional flow of the xylem guarantees effective delivery to the leaves, where nutrients are either stored for later redistribution or used for photosynthesis. In contrast, phloem transport enables bidirectional movement, allowing the pressure-flow mechanism to redistribute nanonutrients from source tissues (such as mature leaves) to sink tissues (like developing grains or roots).

This two-way flow revealed the nanoparticles' mobility in xylem and phloem, which has important ramifications for plant nutrient delivery and redistribution (72). Transmission electron microscopy and energy-dispersive spectroscopy have confirmed that copper oxide nanoparticles (CuO NPs) are absorbed by the roots of maize (Zea mays L.) and transported to the shoots through the xylem. By demonstrating the dual vascular mobility of these nanofertilizers within the plant system and providing direct evidence of root-to-shoot-to-root redistribution, split-root experiments also showed that CuO NPs could travel from shoots back to roots via the phloem (35). A study on the transport of copper, a crucial micronutrient, in the fast-growing woody plant Salix integra revealed that copper was present in both xylem sap and phloem exudate, confirming its long-distance movement via both vascular tissues. Researchers used a radiolabeled copper isotope to demonstrate that copper can be exported through the phloem from mature leaves to new shoots (78 %) and downward to new roots (22 %). This indicates that both xylem and phloem pathways facilitate the efficient and bidirectional redistribution of nutrients (73).

Partitioning into roots, shoots, leaves and grains

The functional impact of nanonutrients on plant growth and nutritional quality is determined by how they are partitioned into the various parts of plants, including the roots, shoots, leaves and grains. Before being transferred to shoots, soil-applied nanonutrients typically first build up in roots, where they may be bound to cell walls or stored in vacuoles (52). In a recent study, barley plants were treated with composite micronutrient nanoparticles comprising nickel, copper, zinc and iron. Analysis conducted after 21 days revealed that these nanoparticles were absorbed and divided into the roots and leaves, with higher concentrations of these elements in both organs resulting from increasing nanoparticle doses. This demonstrates how nanoparticle partitioning can alter nutrient distribution and potentially enhance plant nutritional quality and growth. Interestingly, the highest dose also increased the abundance of some macronutrients (potassium, calcium, magnesium and phosphorus) in the roots, while most of these elements decreased in the leaves (74). Another study examined the effects of nano-enabled fertilisers on rhizosphere processes that affect nutrient partitioning in food crops.

Nanomaterials can enhance the bioavailability and uptake of nutrients, which can subsequently lead to their differential partitioning into various plant parts, including roots, shoots, leaves and grains. The functional impact of nanonutrients on crop productivity and nutrient content was highlighted by the association between improved partitioning, fueled by rhizosphere interactions and increased nutritional quality and growth in food plants (75). Plant species, growth stage and NP characteristics, such as size and surface charge, all affect partitioning patterns. While positively charged NPs, like chitosan-coated nano-urea, exhibit enhanced phloem mobility, resulting in higher grain accumulation, smaller NPs (<20 nm) show greater translocation to aerial parts. Essential elements, like iron in grains for nutritional fortification or zinc in leaves for chlorophyll synthesis, are made available where they are most needed thanks to the differential partitioning of nanonutrients (76).

Interaction with transport proteins and chelation

The movement of nanonutrients within plants is largely dependent on transport proteins and chelation processes, which enable effective delivery to the areas most critical for growth and development. The uptake and translocation of nutrients released from nanoparticles across cell membranes are actively mediated by specific transport proteins, such as YSL proteins for metal-chelate complexes, NRAMP proteins for manganese and ZIP transporters for iron and zinc. Nanoparticles may also interact directly with host proteins by mimicking their natural ligands or inducing conformational changes in transporter proteins. For example, Zn^{2+} ions released from ZnO nanoparticles are recognized by ZIP transporters, facilitating their entry into the cytoplasm. Recent studies suggest that surface-modified NPs (e.g., chitosan- or citrate-coated) can enhance compatibility with membrane-bound transporters, improving nutrient uptake. Additionally, endocytosis-based transport is also modulated by interactions between nanoparticles and clathrin or aquaporin complexes at the plasma membrane, particularly for ultra-small nanoparticles (<10 nm) (77).

The mechanism of chelation is equally critical. Nanoparticles, especially metal-based ones, can form chelates with organic ligands such as amino acids (e.g., histidine, cysteine), organic acids (e.g., citric, malic acid), or Phyto siderophores. These chelated forms exhibit improved solubility, stability and targeted mobility. For instance, iron nanoparticles chelated with citrate or humic substances exhibited better systemic movement and assimilation in crops such as maize and soybeans. Chelation also reduces nanoparticle aggregation, thereby enhancing bioavailability and lowering phytotoxicity (78). By imitating natural ligands that these proteins recognise, sucrose-coated nanocarriers, for instance, have been demonstrated to utilise sugar membrane transporters in the phloem, significantly enhancing the effectiveness of nanoparticle delivery to roots and other tissues (79). The targeted interactions and chelation processes are essential factors that determine the fate, transformation and long-distance translocation of nanoparticles within plants.. These factors ultimately affect the bioavailability of nutrients and the functional impact of nano-fertilisers on plant nutrition and productivity (80).

Nano nutrients and plant disease resistance

Beyond improving nutrient use efficiency, nano-nutrients also contribute to plant defence against pathogens by triggering innate immune responses. Certain metal-based nano formulations, such as zinc oxide (ZnO), copper oxide (CuO) and iron oxide (Fe_2O_3) nanoparticles, exhibit strong antimicrobial properties and can directly inhibit the growth of fungal and bacterial pathogens (40). Additionally, they activate plant defense mechanisms by enhancing the generation of reactive oxygen species (ROS), stimulating antioxidant enzymes (e.g., superoxide dismutase, catalase, peroxidases) and upregulating pathogenesis-related (PR) genes (81). For instance, ZnO nanoparticles have been reported to suppress *Fusarium* and *Alternaria* species in tomato and wheat, while CuO nanoparticles are effective against bacterial blight (*Xanthomonas oryzae*) in rice (15). These nanoparticles serve a dual role-facilitating plant nutrition and offering protection-making them a promising tool for sustainable and integrated crop disease management.

Methods to study uptake, assimilation and translocation of nanonutrients in plants

Robust analytical methods that can both quantitatively and qualitatively record the distribution, chemical transformation and interaction of nanomaterials with plant tissues are necessary to comprehend their fate within plant systems. These techniques are crucial for clarifying the translocation mechanisms, assimilation patterns and uptake pathways of nanonutrients, allowing scientists to assess their effectiveness and potential environmental effects.

Analytical techniques to study entry, assimilation and translocation of nanonutrients in plants

The analytical techniques discussed in this section are summarized in Table 1, which highlights the strengths and limitations of elemental detection tools used to trace nanomaterials in plant systems. Inductively Coupled Plasma Mass Spectrometry (ICP-MS) is a commonly used elemental detection technique due to its multi-element detection capabilities and ultra-trace sensitivity. For instance, ICP-MS enabled the accurate measurement of zinc uptake in maize treated with ZnO nanoparticles, despite the method's requirement for the destructive digestion of plant tissues (82). Similarly, FeO_4 nanoparticle accumulation in rice has been measured using Atomic Absorption Spectroscopy (AAS), which provides high accuracy for single-element quantification (83).

Transmission electron microscopy combined with energy dispersive X-ray spectroscopy (TEM-EDX) and scanning electron microscopy combined with EDX (SEM-EDX) offer high-resolution spatial mapping for nanoscale localisation. When Arabidopsis is exposed to TiO_2 nanoparticles, TEM-EDX provides insight at the nanometre scale, but it takes a lot of time and requires complex sample preparation Si nanoparticles in wheat can be analysed using SEM-EDX, which provides information on surface morphology and elemental distribution but is unable to identify lighter elements below carbon (84).

X-ray fluorescence (XRF), when applied to canola plants treated with CeO_2 nanoparticles, offers a non-destructive alternative with minimal sample preparation (53). When used in soybean studies with Ag nanoparticles, ICP-OES (Inductively Coupled Plasma Optical Emission Spectroscopy) enables robust multi-element detection; however, it necessitates full sample digestion, which introduces matrix effects (85). Although it lacks elemental specificity, Raman Spectroscopy is excellent at determining the structural characteristics of materials, such as carbon nanotubes in mung beans, without destroying the sample in the field of carbon-based nanomaterials. Studies on Arabidopsis have demonstrated that fluorescence spectroscopy is highly sensitive and specific for

Table 1. Analytical and elemental detection techniques for the nanomaterials inside the plant system

Nanomaterials	Plant Studied	Methods / Instruments	Advantages	Limitations	References
ZnO nanoparticles	*Zea mays* (Maize)	ICP-MS (Inductively Coupled Plasma Mass Spectrometry)	High sensitivity, quantitative elemental analysis	Requires digestion of plant tissue; destructive	(93)
Fe_3O_4 nanoparticles	*Oryza sativa* (Rice)	AAS (Atomic Absorption Spectroscopy)	Accurate metal ion quantification	Limited to single element detection	(83)
TiO_2 nanoparticles	*Arabidopsis thaliana*	TEM-EDX (Transmission Electron Microscopy with EDX)	Elemental localization at nanoscale resolution	Expensive, labor-intensive, requires ultrathin sections	(94)
CeO_2 nanoparticles	*Brassica napus* (Canola)	X-ray Fluorescence (XRF)	Non-destructive elemental analysis, minimal sample prep	Lower sensitivity for lighter elements	(53)
Si nanoparticles	*Triticum aestivum* (Wheat)	SEM-EDX (Scanning Electron Microscopy with EDX)	Surface morphology with elemental composition	Cannot detect elements below atomic number 6 (C)	(84)
Ag nanoparticles	*Glycine max* (Soybean)	ICP-OES (Optical Emission Spectroscopy)	Multi-element analysis, robust data	Requires complete digestion; matrix effects	(113)
Carbon nanotubes	*Vigna radiata* (Mung bean)	Raman Spectroscopy	Non-destructive, identifies structural properties of carbon-based nanomaterials	Limited elemental specificity	(114)
Quantum dots	*Brasdopsis thaliana*	Fluorescence Spectroscopy	Specific and highly sensitive for fluorescent nanoparticles	Limited to fluorescent materials only	(86)

fluorescent nanomaterials, such as quantum dots; however, it is only useful for substances that are naturally fluorescent (86).

Isotope tracing techniques for studying uptake and translocation of nanonutrients in plants

An accurate and trustworthy way to investigate the uptake, assimilation and translocation of nanonutrients within plant systems is through the use of isotope tracing techniques. Researchers can track the movement of nanoparticles from the application site through different plant organs and, in certain situations, into the food chain by labelling them with stable or radioactive isotopes. These methods help clarify how nanofertilizers behave in plants in authentic environmental settings. Radioisotope labelling, such as the use of ^{64}Cu to track CuO nanoparticles in lettuce, is a popular method. Research indicates that autoradiography can be used to visualise the mobility and uptake pathways of nanoparticles within leaf tissues (87). ^{29}Si-labeled Ag nanoparticles were employed in soybeans in a more chemically stable application, where silicon was monitored using nuclear magnetic resonance (NMR) spectroscopy from roots to leaves (88).

Isotope Ratio Mass Spectrometry (IRMS) has demonstrated promise in tracking foliar uptake and systemic translocation through stable isotope techniques, such as ^{2}H-labeled nanoplastics in lettuce. Research indicates the need to examine trophic transfer through food chains (89). Similarly, to evaluate carbon assimilation and nanoparticle distribution, IRMS and TOF-SIMS were used to track ^{13}C-labeled fullerenol nanoparticles in wheat (78). For fullerene (C_{60}) applications in various crops, a dual-isotope labelling approach utilising ^{15}N and ^{13}C was employed. Here, their impact on nitrogen and mineral uptake was assessed using IRMS and Synchrotron Radiation micro-X-ray Fluorescence (SR-µXRF) (90). Raven (91) points out that in more sophisticated nano-tracking systems, nutrient-coated quantum dots with specially labelled isotopes offer both fluorescent and isotopic tracing capabilities, providing a dual-modality approach for both quantitative and spatial analysis. Using single-particle ICP-MS, trace metals such as selenium were detected in plants using ^{78}Se and ^{82}Se isotope-labelled Se nanoparticles. The results showed that the nanoparticles were absorbed and distributed with high sensitivity and elemental specificity (92). A detailed comparison of isotope tracing techniques, isotopes used and instruments applied across different plant systems is provided in Table 2, showing how isotopic labelling enables precise and quantitative tracking of nanoparticle movement.

Imaging techniques to study uptake, assimilation and translocation of nanonutrients in plants

Imaging methods used for intracellular localisation, 3D mapping and vascular tracking of nanoparticles are compiled in Table 3, which includes TEM, SEM, MRI and micro-XRF techniques applied to crops such as Arabidopsis, maize and soybean. High-sensitivity quantitative information on the metal content of plant tissues can be obtained using elemental detection methods, such as Atomic Absorption Spectroscopy (AAS) and Inductively Coupled Plasma Mass Spectrometry (ICP -MS). For example, ZnO nanoparticles in maize were traced using ICP-MS (93) and FeO_4 in rice was quantified using AAS (83). These techniques are typically harmful and often require the acid digestion of plant tissues. As demonstrated in canola plants treated with CeO_2 NPs, alternative methods such as X-ray fluorescence (XRF) provide non-destructive analysis (53). For the surface and intracellular localisation of Si and TiO_2 nanoparticles, respectively, SEM-EDX and TEM-EDX combine morphological visualisation with elemental mapping (84).

Elemental detection techniques such as Atomic Absorption Spectroscopy (AAS) and Inductively Coupled Plasma Mass Spectrometry (ICP-MS) can provide high-sensitivity quantitative data on the metal content of plant tissues. For instance, FeO_4 in rice was measured using AAS (83) and ZnO nanoparticles in maize were traced using ICP-MS (93). These methods often require the acid digestion of plant tissues and are generally harmful. Alternative techniques, such as X-ray fluorescence (XRF), offer non-destructive analysis, as demonstrated in canola plants treated with CeO_2 NPs (53). SEM -EDX and TEM-EDX combine elemental mapping and morphological visualisation for the surface and intracellular localisation of Si and TiO_2 nanoparticles, respectively (84, 94).

Spectroscopic and molecular techniques to study nanonutrient behavior in plants

An overview of the plant systems, instruments and methodological outcomes for molecular and spectroscopic techniques is presented in Table 4. This includes qPCR, FTIR, XRD and Raman spectroscopy-based insights into the interaction of nanomaterials with plant biomolecules. Spectroscopic and molecular techniques are essential for revealing the interactions, localisation, gene expression and biochemical reactions of plants exposed to nanonutrients.

Table 2. Isotope tracing techniques for studying uptake and translocation of nanonutrients in plants

Nanomaterials / Nanofertilizer	Plant studied	Isotopes	Instrument	Remarks	References
CuO nanoparticles	*Lactuca sativa* (Lettuce)	^{64}C	Autoradiography	Tracked uptake routes and mobility within leaf tissue	(87)
Ag nanoparticles	*Glycine max* (Soybean)	^{29}Si	NMR (Nuclear Magnetic Resonance)	Monitored Si translocation from roots to leaves	(88)
Nanoplastics (D-labelled)	*Lactuca sativa* (Lettuce)	^{2}H (Deuterium)	Isotope Ratio Mass Spectrometry (IRMS)	Tracked foliar uptake, systemic transport and trophic transfer	(89)
Fullerenol nanoparticles	*Triticum aestivum* (Wheat)	^{13}C	IRMS, TOF-SIMS	Measured bioaccumulation and carbon assimilation	(10)
Fullerene (C_{60})	Multiple crops	^{15}N, ^{13}C	SR-µXRF, IRMS	Studied nanoparticle influence on nutrient uptake via stable isotope tracing	(90)
Quantum Dot Nutrients	General (review-based)	Custom-labeled isotopes	Fluorescence + Mass Spectrometry	Commentary on isotopic nutrient tracking using QDs in plant systems	(91)
Selenium nanoparticles	Not specified (general plants)	^{78}Se, ^{82}Se	Single-Particle ICP-MS	Traced Se-NP uptake and distribution via isotope-labeled	(92)

Table 3. Imaging techniques employed for the detection of nanomaterials inside the plant system

Nanomaterials / Nanofertilizer	Plant studied	Instrument	Maximum depth	Remarks	References
TiO_2 nanoparticles	*Arabidopsis thaliana*	Transmission Electron Microscopy (TEM)	< 100 nm	Visualized intracellular localization and vesicle encapsulation	(115)
ZnO nanoparticles	*Zea mays* (Maize)	Scanning Electron Microscopy (SEM)	Surface only	Observed surface adsorption and root morphology	(116)
Fe_3O_4 nanoparticles	Tomato	Magnetic Resonance Imaging (MRI)	Several mm	Non-invasive detection of magnetic nanoparticles in vascular tissue	(117)
TiO_2 nanoparticles	*Cucumis sativus* (Cucumber)	X-ray Fluorescence (micro-XRF) and Micro X-ray Absorption Near Edge Structure (micro-XANES)	-	Provided 3D mapping of TiO_2 NPs in roots and stems	(81)
Carbon Quantum Dots	*Glycine max* (Soybean)	Fluorescence Microscopy	200 µm	Enabled tracing through stomatal and vascular entry routes	(118)
TiO_2 nanoparticles	*Triticum aestivum spp.*	Transmission Electron Microscopy (TEM)	655 nm	Visualized intracellular localization and vesicle encapsulation	(119)

Table 4. Spectroscopic and molecular techniques employed for the detection of nanomaterials inside the plant system

Nanomaterials / Nanofertilizer	Plant studied	Instrument	Methodology	Remarks	References
ZnO nanoparticles	*Oryza sativa* (Rice)	FTIR, UV-Vis	FTIR spectral analysis, absorption spectra	Confirmed interaction with functional groups and uptake	(95)
Fe_3O_4 nanoparticles	*Glycine max* (Soybean)	qRT-PCR	Gene expression profiling	Upregulation of stress-related genes	(98)
TiO_2 nanoparticles	*Oryza sativa* (Rice)	Raman Spectroscopy	Vibrational spectroscopy	Tracked TiO_2 localization via Raman signal	(97)
Chitosan nanofertilizer	*Triticum aestivum* (Wheat)	FTIR, SEM-EDX	FTIR + elemental analysis	Studied nutrient interactions and surface morphology	(100)
Nano-hydroxyapatite	*Brassica napus*	XRD, UV-Vis	Crystallinity + nutrient release kinetics	Verified nutrient release and interaction with plant tissue	(96)
SiO_2 nanoparticles	*Cucumis sativus* (Cucumber)	PCR, SDS-PAGE	Protein profile and stress gene expression	Altered protein profile under nanoparticle treatment	(99)
CeO_2 nanoparticles	*Lactuca sativa* (Lettuce)	ICP-OES, FTIR	Elemental uptake + bonding interaction	Quantified Ce uptake and assessed biochemical interactions	(44)
Carbon Nanotubes (CNTs)	*Spinacia oleracea* (Spinach)	Microarray, RT-PCR	Global gene expression profiling	CNTs induced changes in transcriptomic profiles	(120)
CuO nanoparticles	*Solanum lycopersicum* (Tomato)	UV-Vis, ICP-MS	Optical & elemental analysis	Evaluated antioxidant response and Cu uptake	(2)

Determining uptake patterns, biochemical assimilation and the ensuing physiological and molecular reactions triggered by nanoparticle exposure all depend on these methods. Two commonly used methods to ascertain how nanoparticles interact with functional groups in plant tissues are UV-Vis spectroscopy and Fourier Transform Infrared Spectroscopy (FTIR). For instance, ZnO nanoparticles in rice displayed characteristic FTIR peaks that confirmed their attachment to biochemical moieties (95). Similarly, XRD and UV-Vis spectroscopy demonstrated the nutrient release kinetics and crystallinity of nano-hydroxyapatite, confirming its gradual assimilation by *Brassica napus* (96).

Raman spectroscopy served as a vibrational probe for the localisation of nanoparticles on rice treated with TiO_2, negating the need for labelling (97). For elemental quantification and further internalisation confirmation, maize exposed to silver nanoparticles was subjected to Inductively Coupled Plasma Mass Spectrometry (ICP-MS). Changes in gene expression in defence-related pathways were assessed using quantitative PCR (qPCR). Molecular methods, such as qRT-PCR and microarray, can be used to profile changes in gene expression induced by nanomaterials. For example, FeO_4 nanoparticles caused the upregulation of genes related to stress in soybeans, while carbon nanotubes in spinach altered global transcriptomic profiles associated with growth and defence (98). Using PCR and SDS-PAGE to track changes in gene and protein expression caused by SiO_2 exposure in cucumbers showed how nanomaterials can be integrated at both the genomic and proteomic levels (99). Furthermore, SEM -EDX in combination with FTIR was used to examine surface interactions and nutrient availability from chitosan nanofertilizers in wheat (100). These combinatorial techniques offer both quantitative and qualitative data regarding the physiological impacts and absorption of nanofertilizers.

In addition to their individual capabilities, the integration of spectroscopic and molecular approaches enables deeper mechanistic insights into how nanonutrients interact with plant biomolecules and gene regulatory networks. For example, FTIR and Raman spectroscopy can be employed in tandem to capture both functional group interactions (via FTIR) and structural or vibrational changes (via Raman) that occur upon nanoparticle binding or assimilation within plant tissues (78). This is particularly valuable in determining whether nanoparticles bind covalently or through weak electrostatic interactions to proteins, lipids, or cell wall polysaccharides. Moreover, molecular tools such as qRT-PCR and transcriptome profiling help validate whether such nanoparticle interactions translate into altered expression of genes related to stress, transport, or metabolism. Techniques like SDS-PAGE and western blotting, although less frequently used, can track post-translational modifications or protein-level responses to nanoparticle exposure (101). Importantly, the use of nanoparticle-specific probes or primers, as well as reference genes for normalization, is critical

Table 5. Physiological and biochemical techniques to understand the assimilation and efficacy of nanofertilizers

Nanomaterials / Nanofertilizer	Plant studied	Methodology	Remarks	References
ZnO nanoparticles	*Triticum aestivum* (Wheat)	Measurement of chlorophyll, photosynthetic rate, MDA and proline content	ZnO improved photosynthesis and antioxidant defense, reduced oxidative stress	(103)
TiO_2 nanoparticles	*Oryza sativa* (Rice)	ROS quantification, antioxidant enzyme assays (SOD, CAT, POD)	TiO_2 NPs triggered antioxidant responses and modulated reactive oxygen species	(104)
Fe_3O_4 nanoparticles	*Zea mays* (Maize)	Electrolyte leakage, chlorophyll content, nitrate reductase activity	Improved growth and physiological stability under stress	(105)
Chitosan nanofertilizer	*Solanum lycopersicum* (Tomato)	Proline, soluble sugar content, peroxidase activity	Enhanced drought tolerance via osmolyte accumulation and enzyme induction	(101)
Nano-silicon	*Cucumis sativus* (Cucumber)	Stomatal conductance, RWC, lipid peroxidation assays	Improved water retention and reduced cell membrane damage under drought	(106)
Carbon Nanotubes (CNTs)	*Spinacia oleracea* (Spinach)	Enzyme activity profiling, ROS detection	CNTs enhanced enzymatic antioxidant activity and nutrient assimilation	(107)
Ag nanoparticles	*Lactuca sativa* (Lettuce)	Electrolyte leakage, H_2O_2 and proline estimation	Demonstrated dose-dependent phytotoxicity and altered membrane stability	(108)
CeO_2 nanoparticles	*Brassica napus*	Lipid peroxidation (MDA), antioxidant enzyme levels	CeO_2 NPs mitigated oxidative stress and improved photosynthetic efficiency	(121)
Phosphorus nano-fertilisers	*Arabidopsis thaliana*	Leaf area, dry biomass and phosphorus content	Promoted P uptake and improved physiological performance	(109)

for accurate molecular interpretation (102). Collectively, this technical layering of spectroscopic and molecular approaches not only confirms the presence and distribution of nanomaterials but also reveals the biological consequences of their assimilation, providing a comprehensive understanding of nanofertilizer-plant interaction dynamics.

Physiological and biochemical techniques to assess nanofertilizer assimilation and efficacy

Table 5 provides a comparative overview of physiological and biochemical assays used to assess the efficacy of nanofertilizers in various crops, focusing on antioxidant responses, photosynthesis, nitrogen metabolism and drought adaptation. To evaluate the assimilation and systemic efficacy of nanofertilizers in plant systems, a range of physiological and biochemical methods are employed. These methods provide insight into how nanomaterials affect cellular and whole-plant nutrient assimilation, stress responses and plant metabolism. Measuring oxidative stress indicators, chlorophyll content and photosynthetic parameters is a primary tactic. For instance, ZnO nanoparticles improved photosynthetic efficiency and antioxidant defence in wheat by increasing chlorophyll concentration and lowering proline and malondialdehyde (MDA) levels (103). By modifying reactive oxygen species, TiO_2 nanoparticles also increased the activity of antioxidant enzymes in rice, including SOD, CAT and POD, reducing oxidative stress (104).

Fe_3O_4 nanoparticles in maize exhibited improved physiological stability and enhanced nitrogen assimilation by modulating nitrate reductase activity, electrolyte leakage and chlorophyll content (105). Tomatoes treated with chitosan-based nanofertilizers exhibited a significant increase in proline and soluble sugar content, accompanied by an increase in peroxidase activity. This improvement in drought tolerance was achieved through osmotic regulation and stress adaptation (101). Other nanomaterials, such as nano-silicon, have been demonstrated to contribute to the preservation of water status and membrane integrity in cucumbers by increasing stomatal conductance and relative water content (RWC) and decreasing lipid peroxidation during drought (106). Carbon-based nanomaterials, such as carbon nanotubes (CNTs), also enhance nutrient absorption and antioxidant enzyme activity in spinach, suggesting that they have a dual function in reducing stress and improving metabolism (107). Conversely, Ag nanoparticles increased H_2O_2 accumulation and electrolyte leakage in lettuce, demonstrating dose-dependent phytotoxicity and emphasising the need to balance plant type and dosage (108). Finally, CeO_2 nanoparticles enhanced photosynthesis and decreased oxidative stress in canola by suppressing lipid peroxidation and boosting the expression of antioxidant enzymes, while nano-phosphorus fertilisers increased P uptake and biomass in Arabidopsis (109).

Dyeing and labelling techniques for tracing nanonutrient movement in plants

Tracking the real-time movement and localization of nanofertilizers within plant systems is a critical step in understanding their uptake efficiency, translocation dynamics and eventual assimilation or accumulation in tissues. Dyeing and labelling techniques-especially fluorescence-based approaches-have emerged as powerful, non-destructive tools for visualizing and validating nanoparticle behaviour inside plants. The fluorescent labelling methods, dyes used and plant -specific applications are summarized in Table 6, showcasing their role in tracking systemic uptake and confirming entry routes through confocal and fluorescence microscopy. These methods complement elemental and isotopic analyses by offering spatial and temporal resolution, making them indispensable in nano-agriculture research (78). Fluorescent dyes such as Rhodamine B, FITC (fluorescein isothiocyanate) and Rhodamine 6G are often conjugated to nanoparticles or incorporated into nanocarriers to track their movement under fluorescence or confocal microscopy. These tagged nanoparticles can reveal detailed intracellular movement, including entry routes (e.g., stomata, cuticle), tissue distribution (e.g., root cortex, xylem, mesophyll) and systemic translocation to shoots and grains (110). For instance, Rhodamine B-labelled CuO nanoparticles have demonstrated the ability to penetrate through stomata in rice, thereby confirming foliar entry mechanisms.

In addition to exogenous dyes, intrinsically fluorescent nanoparticles such as quantum dots (e.g., CdSe/ZnS) and

Table 6. Dyeing and labelling techniques to track the movement of the nanomaterials inside the plant system

Nanomaterials / Nanofertilizer	Plant studied	Dye	Remarks	References
Chitosan nanoparticles	*Solanum lycopersicum*	Rhodamine B	Tracked intracellular distribution in roots and shoots	(122)
Mesoporous silica nanoparticles	*Arabidopsis thaliana*	Fluorescein isothiocyanate (FITC)	Visualized endocytosis and vascular transport	(123)
Palladium nanoparticles	*Azadirachta indica*	Rhodamine 6G	Enabled visualization of foliar absorption and translocation	(124)
Silica nanoparticles	*Glycine max* (Soybean)	FITC	FITC-labeled SiNPs localized in the cytoplasm and cell walls	(125)
Quantum dots	*Arabidopsis thaliana*	CdSe/ZnS (intrinsic fluorescence)	Monitored uptake and intracellular localization via intrinsic photoluminescence	(86)

carbon-based nanomaterials enable label-free imaging with higher stability and reduced photobleaching. These materials enable the precise tracking of nanoparticle localisation within cellular compartments (e.g., cytoplasm, vacuoles, organelles) without the need for additional chemical labelling (111). Moreover, these techniques support quantitative uptake studies when combined with intensity calibration and time-lapse imaging. When integrated with other tools (e.g., elemental mapping, TEM), fluorescence imaging confirms co-localization and uptake pathways (42). Recent innovations also include dual-mode tracers (e.g., isotope and dye, or fluorescence and MRI) to enhance both spatial tracking and quantitative resolution.

However, challenges remain in dye leaching, photobleaching and interference with plant autofluorescence. Therefore, appropriate controls and calibration curves are necessary (112). Despite these limitations, dyeing and labelling techniques offer an accessible and visual gateway to understanding nanofertilizer dynamics in planta and are increasingly being used for regulatory, ecological and formulation optimization purposes.

Conclusion and Future perspectives

The use of nanotechnology in agriculture through the application of nanonutrients represents a groundbreaking approach to addressing nutrient inefficiency, environmental pollution and promoting sustainable crop production. The current database demonstrates that nanonutrients are effectively taken up by plants through either root or foliar treatments and distributed to target tissues, where they are integrated into metabolic pathways with greater efficiency compared to conventional fertilisers. Across species such as maize, soybean, tomato, rice and barley, nanonutrients have demonstrated positive physiological and biochemical regulation, validating their cross-crop utility and justifying broader research into crop-specific responses. Yet, their physicochemical fate and behaviour in the plant system are highly dependent on their physicochemical nature, mode of application, the plant and environmental conditions. Even with significant progress, the specific mechanisms underlying nanonutrient uptake, modification and long-distance transport remain largely unknown. Methodological progress, including the utilisation of isotope tracing, high-resolution microscopy, molecular profiling and spectroscopic analysis, has significantly enhanced the ability to trace and characterise nanomaterials within plant systems. Standardisation of protocols and the implementation of non-destructive, high-throughput methods are essential to improve data reproducibility and facilitate cross-study comparisons. Future studies should focus on: (i) Designing biocompatible and biodegradable nanocarriers with low toxicity and high nutrient bioavailability. (ii) Understanding nanoparticle-plant-microbe interactions in real field environments. (iii) Applying omics-based platforms (transcriptomics, metabolomics, proteomics) to unravel the molecular process of nanonutrient uptake. (iv) Establishing regulatory frameworks and environmental risk assessments to ensure the safe and sound use of nanofertilizers. A multidisciplinary approach, involving plant physiology, nanotechnology, analytical chemistry and environmental science, will be critical to unlocking the full potential of nanonutrients in precision and sustainable agriculture.

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Authors' contributions

MK led the original draft writing. GV provided supervision and contributed to the review and editing. GG, MS and KP were involved in the critical review and editing of the manuscript. RS and SN participated in reviewing and refining the manuscript content. All authors reviewed and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no other competing interests.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors utilised ChatGPT by OpenAI to assist with language refinement for clarity. After using this tool, the authors reviewed, validated and edited the content as needed, taking full responsibility for the integrity and accuracy of the final version of the publication.

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