

Review Article

Uptake, Translocation, and Consequences of Nanomaterials on Plant Growth and Stress Adaptation

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Nanotechnology has shown promising potential tools and strategies at the nanometer scale to improve food production and meet the future demands of agricultural and food security. However, considering nanotechnology's potential benefits to date, their applicability has not yet reached up to field conditions. Increasing concerns regarding absorption, translocation, bioavailability, toxicity of nanoparticles, and impropriety of the regulatory framework restrict the complete acceptance and inclination of the agricultural sector to implement nanotechnologies. The biological function of nanoparticles depends on their physicochemical properties, the method of application, and concentration. The effects of the various types of nanoparticles (NPs) on plants were determined to increase seed germination and biomass or grain yield. The NPs also increased the plant's resistance to various biotic and abiotic stresses. The plant's biological functions depend on the events that occur at the molecular level. However, little progress has been made at the molecular level influenced by nanoparticles, which is an important step in evaluating potential mechanisms and plants' effects. Therefore, it is important to understand plants' underlying mechanism and response towards nanoparticles, and the gene expression changes through molecular approaches. The associations of nanomaterials with plant cells, the process of internalization, and the distribution of biomolecules using nanoparticles as a carrier are studied but not well understood. The transmission of biomolecules, such as nucleic acids, is a major obstacle due to cell walls, limiting the application of nanomaterials in crop enhancement mediated by genetic engineering. Recently, the use of different nanomaterials for nucleic acid delivery in plant cells has been published. Here, we aim to update researchers on the absorption and translocation of nanoparticles and elaborate on the importance of nanoparticles in agriculture and crop stress tolerance.

1. Introduction

Significant technical advancements and innovations have been made in recent years in agriculture to meet the growing challenges of sustainable agricultural production and food security [1, 2]. The world needs to generate 50% more food by 2050 to meet the needs of 9 billion people. This goal can only be accomplished by technical interventions to increase productivity, as land and water resources are constrained. Arable land shortage, irrigation, and reliance on conventional crops are the key concerns that have drawn the researchers' attention to using various methods. It is not surprising that attempts have been made to improve the agricultural sector using nanotechnology and nanomaterials

because of nanomaterials' obvious special and incredible properties [3–5]. In particular, the use of different kinds of nanomaterials consists of metal oxides, silicates, ceramics, magnetic materials, semiconductors of quantum dots (QD), polymers, lipids, dendrimers, and emulsions [6–8]. The goals are to minimize the quantity of applied plant protection products (PPP), alleviate nutrient losses during fertilization, and maximize revenue in the agriculture sector through better nutrient management [9]. Many factors depend on the increased use of nanoparticles (NPs) in agriculture, including well-known effects, potential toxicity, monitored fate, and overdose levels. NPs can communicate with their environment, and plants are a key component of all ecosystems. Therefore, it can be concluded that NPs can communicate

with plants and that these interactions, such as their intake and their accumulation in plant biomass, will affect their environmental fate and transport [10–12]. Nanomaterials can penetrate live plant tissues, but their aggregation in the ecosystem and their effectiveness as smart delivery systems in living plants have implications. It is important to understand whether plants can consume intact NPs and transport them to other plant tissues. NPs can enter plant tissue from either the root tissues or the above-ground tissues (e.g., cuticles, stomata, hydathodes, and trichrome) as well as through root junction and wound regions.

Nanomaterials in plant science have been reported to enhance agronomic capabilities [13–15]. NPs are used as sensing materials [14, 15], herbicides, pesticides, and nanofertilizers [16, 17], improve the plant nutrients, and act as carriers for controlled release of agrochemical [18–20]. Nanomaterials also speed up plant adaptation to various climatic changes and enhance plant tolerance [21, 22]. However, certain nanoparticles (NPs) with unique physiochemical properties naturally increase plant growth and stress resistance rather than acting as nanocarriers. The biological function of nanoparticles depends on their physicochemical properties, the application method (soil, foliar, and hydroponics), and the used concentration. Nanomaterials have also demonstrated their prominent role in plant tissue *in vitro* cultures, such as callus induction, organogenesis, somatic embryogenesis, and secondary metabolite production [23]. Such studies suggest that plant cells can accumulate nanoparticles through their cell walls, but the mechanism is still not well understood. Although the use of nanomaterials for DNA delivery in plant cells has also been studied in the past [24], substantial developments have been made in recent years.

This study is aimed at examining in detail the role of nanotechnology in the delivery of NPs, the use of NPs in improving seed germination, and plant growth under both natural and environmental stress conditions. In addition, we elaborate the nanotechnology's current advances and associated challenges.

2. Absorption and Translocation of Nanoparticles

2.1. Mechanisms of Nanoparticle Uptake by Plants. In the soil, the NPs undergo a series of bio/geotransformations, which determine the bioavailability and toxicity of NPs. The NPs translocate to aerial portions after interacting with plant roots and accumulate in cellular or subcellular organelles. Adsorption of NPs from the soil by plant roots can be described as the first step in bioaccumulation [25]. Several researchers analyzed numerous NPs and proposed that plant accumulation occurred by root adsorption accompanied by dissemination through plant tissues by certain modifications, such as crystal phase dissolution, biotransformation, and bioaccumulation. The NP's size is directly connected to the absorption of the NPs because it is a crucial parameter that enables its entrance through cell wall pores or plant stomata. Besides, size determines their subsequent transport processes into cells (i.e., plasmodesmata) or organelles of plant cells,

affecting their accumulation, toxicity, and kinetics of transport into plant cells [22]. The surface area, agglomeration, and reactivity on the cell surface or within plant structures are correlated with the NP shape [26]. To determine the specific zone of interaction between plant cell structures and NPs, the NP surface is calculated by its area and morphology, which constitute essential parameters. Due to the obvious negative charge of the cell wall, the attachment of the NPs to the surface of the plant cell relies directly on the charge of the NPs. Following the charge and particle size, the hydrophobicity present on the plant surface played a crucial role in the uptake and translocation process [27]. In addition, the basic structure of nanomaterials is complementary to the evaluation of their effect on NP absorption, translocation, and aggregation in the plant [28]. The above facts demonstrate the need to standardize laboratory experiments to assess NPs in plant tissues at various levels to determine the exact effect of NPs supported by their physical-chemical properties [29]. Therefore, to understand and elucidate the absorption, translocation, and accumulation processes, a detailed study on the nature of the NPs is needed. To determine their movement and localization to various structures and cell organelles within the plant, monitoring and tracking NPs are important.

The small NPs (diameters range from 3 to 5 nm) are reported to penetrate plant roots along with osmotic pressure, capillary forces, or passing directly through the root epidermal cells [30, 31]. The epidermal cells of the root cell wall are semipermeable containing small pores and restrict the large NPs. Some NPs induced new pores in the epidermal cell wall, which facilitated its entrance [30, 31]. After crossing the cell walls, NPs are apoplastically transported through extracellular spaces until they reach the central vascular cylinder, allowing the xylem to move unidirectionally upward. NPs, however, need to symplastically cross the Casparian strip barrier to enter the central vascular cylinder (Figure 1). This happens by binding to the endodermal cell membrane's carrier proteins through endocytosis, pore formation, and transport. NPs travel from one cell to another through the plasmodesmata as internalized in the cytoplasm [22, 32]. The NPs unable to internalize are aggregate on the Casparian strip, while the NPs that have reached to xylem are transferred to the shoots and through the phloem back to the roots [32, 33]. NPs taken up by plants may be found within the epidermal cell wall, cortical cell cytoplasm, and nuclei [33]. NPs that are not taken up on the soil aggregate's root surface can modify the absorption of nutrients [34]. Direct absorption of NPs in seeds can occur by entering the coat via parenchymatic intercellular spaces, accompanied by diffusion in the cotyledon [22].

The NPs applied by the leaves can enter the leaves through the stomata or cuticles. The cuticle acts as a primary leaf barrier, restricting the entry of NPs to a size of <5 nm. The NPs > 10 nm enter through stomata, and their cellular transport is occurring through apoplastic and symplastic routes into the vascular system of the plant [34]. The transfer of NPs (between 10 and 50 nm) is favored through the adjacent cell's cytoplasm (symplastic route). Thus, larger NPs (between 50 and 200 nm) are translocated between the cells

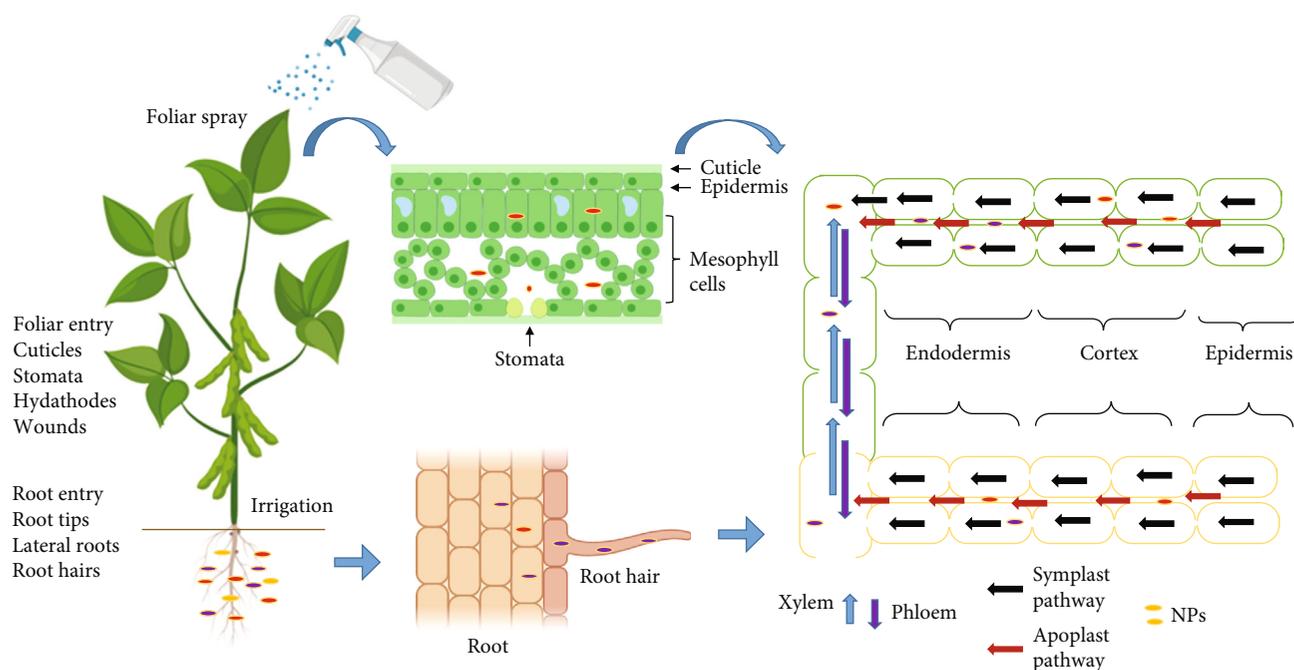


FIGURE 1: Schematic presentation of nanoparticle uptake through different routes and their translocation pathways in different plants' parts.

(apoplastic route). Internalized NPs are transported along with the sugar flow through the phloem sieve tubes. As a result of vascular transport by phloem, NPs can travel bidirectionally and accumulate in roots, stems, fruits, grains, and young leaves to varying degrees because these organs serve as potent sinks for the sap [22, 26, 28, 34]. The apoplastic passage is known as a nonselective direction of least resistance. It is widely agreed that many water nutrients and nonessential metal complexes favor the apoplastic route for translocation [35]. The application methods, size, concentration, and climate are the essential factors that determined the effective adsorption of NPs after foliar application [26]. Leaf morphology and its chemical composition, the presence of trichome, and existence of leaf exudates and waxes are essential factors that affect the trapping of NPs on the surface of the leaf [36].

It is important to introduce NPs of high purity and stability to the physiological environment. The accumulation rate of NPs by the root of plants may be impacted by environmental conditions and the properties of NPs. Previous studies reported that the application of silver sulfide (Ag₂S) NPs in combination with potassium chloride and ammonium thiosulfate significantly enhanced the concentration of Ag NPs in the shoot and roots of *Lactuca sativa*. (Table 1) [37]. Soil organic matter decreased cerium dioxide (CeO₂) NPs through roots in *Zea mays* (*Z. mays*) [38].

2.2. Mechanism of Nanoparticle Translocation in Plants. Studies attempted to establish the mechanisms involved in plant structures or cell organelles in the absorption, translocation, and accumulation of various NPs [27]. The translocation and accumulation of NPs in the plant depend on the plant cells' physiology and structure, the nanomaterial interaction with the soil, and the nature and stability of the NPs

[39]. The cell wall of plants serves as a specific barrier that regulates the entrance of NPs into the cell and determines the ability to solubilize and allow the passage of NPs according to their nature [40, 41]. The majority of studies report that the size of the cell wall's pore is the key constraint on the entrance of NPs into the plant cell. The size of NPs is 40-50 nm to penetrate the cell from the plant surface [42]. The nature of the NPs is a second restriction factor impacting their penetration through the cell wall and cell membrane or promoting attachment to the radical surface or radical exudates [43]. The positive charging of NPs can improve their adhesion to the cell wall. Besides, morphology and NP coating can play a significant role in their behavior on the rhizosphere and their action on plants.

The nanoparticles accumulated by plant roots translocate to different tissues in the plant's aerial part, including newly developed seeds [22]. Plant characteristics and NPs all play a crucial role in the translocation of NPs. For example, previous studies have shown that gold (Au) NPs can accumulate in the shoot of *Oryza sativa* (*O. sativa*). In contrast, it cannot accumulate in the shoot of *Cucurbita pepo* and *Raphanus raphanistrum* [44]. Furthermore, plant roots take up the positively charged Au NPs most quickly.

In contrast, negatively charged Au NPs are translocated from the roots more resourcefully into plant shoots. Previous studies reported that titanium dioxide (TiO₂) and silicon dioxide (SiO₂) are the most stable NPs and can be found in their immaculate speciation in plant tissues [57, 58]. NPs like copper (II) oxide (CuO), CeO₂, lanthanum oxide (La₂O₃), and nickel oxide (NiO) are capable of transformation through disparity, resulting in accumulated plant speciation changes. The transformations of zinc oxide (ZnO) NPs were determined using synchrotron X-ray absorption (XAS) spectroscopy during exposure to different plants [59]. In *Z. mays*,

TABLE 1: Accumulation of NPs in various crop tissues.

NPs	Crops	Concentration (mg/L * mg/kg)	Accumulation (mg/kg)		References
			Roots	Shoots	
Ag-based	<i>O. sativa</i>	1000	20	5	[45]
	<i>Glycine max</i>	4000	2102	1135	[46]
	<i>Solanum lycopersicum</i>	250	—	50	[47]
Cu-based	<i>O. sativa</i>	1000	1544.1	17.27	[48]
	<i>B. juncea</i>	1500	190.4	—	[49]
	<i>Cajanus cajan</i>	20	5.82	19.06	[50]
	<i>Vigna radiata</i>	125	—	18.46	[51]
	<i>L. sativa</i>	250	3773	—	[52]
	<i>Phaseolus vulgaris</i>	100	800	—	[53]
ZnO	<i>S. lycopersicum</i>	1000	—	250	[54]
	<i>Z. mays</i>	100	10	30	[55]
Mg(OH) ₂	<i>Z. mays</i>	1000	103	131	[56]
TiO ₂	<i>S. lycopersicum</i>	1000	—	250	[54]

the maximum accumulation of Zn occurs in the roots and shoots under the hydroponic exposure of ZnO NPs in various forms such as Zn-phosphate. It may be due to increased dissolution in the rhizosphere, plant absorption, and translocation of Zn in the ionic form [55]. Comparable Zn accumulated speciation was also observed in soil-grown wheat crops [60, 61].

Translocation from the soil of ZnO and CeO₂ NPs into *Glycine max* (*G. max*) had been observed. The CeO₂ NPs were revealed to be translocated in the form of NPs, and Zn biotransformed into Zn-citrus inside plant tissue [46]. The transport of CuO NPs from roots to shoots via xylem took place in *Z. mays* and could be further translocated from shoots back to roots via the phloem back to roots [33]. Previous studies concluded that NP TiO₂ plays a role in the translocation in the *Triticum aestivum* (*T. aestivum* spp.). They proposed that a threshold diameter of 140 nm, above, cannot accumulate in the root. In addition, a threshold diameter of 36 nm can accumulate in the root parenchyma, could not reach the stele, and cannot be translocated into the shoot of *T. aestivum* [62].

3. Mechanisms of Nanoparticle and Plant Interaction

3.1. Effects of Nanoparticles on Plants. The NPs enter the plant system by several routes, mainly through roots and leaves. NPs interact with plants at cellular and subcellular levels after entry, promoting changes in morphological and physiological states [63]. These interactions may be positive or negative, depending on the nature of the NPs and the plant species. The chemical nature, reactivity, size, and specifically concentration of NPs in or on the plant could determine NPs' effects on plant systems [64]. The researchers used various NP application methods, such as soil application, foliar spray, or seed treatment, to examine the impact of nanoparticles on seed germination or in plant growth. Available

evidence has shown that different NPs can promote seed germination [65] and plant growth and development [66–68] at concentrations below certain limits. These studies were mostly performed under artificial treatment conditions such as plate growth medium and hydrophobic or pot conditions. To understand the impact of nanoparticles on plant growth, we discuss nanoparticle's positive impact on plant seed germination and plant growth and the positive effects of NPs to improve plant stress tolerance.

3.2. Seed Germination. Germination of seeds provides a basis for the productivity, growth, and development of plants. A natural method of germination takes time, and the yield obtained is not very high indeed. But high germination has been accomplished in the case of treated seeds, making nanotechnology a potent technique for improving both germination and yield. To monitor the ability of nanoparticles to enhance germination, numerous researches have been done. The mechanism underlying the process by which NP treatments increase seed germination rates is still unclear. The NP treatments improve seed absorption and water retention; it may be attributed to increasing seed germination [69]. The tomato seeds were inoculated to media with carbon nanotubes (CNTs); after 2-day incubations, the seeds' moisture content was treated with CNTs containing 19% more than untreated seeds. These findings suggested that the CNTs promote the uptake and retention of water. The mechanism is not fully understood; maybe the CNTs create microspores [70], and water permeation channels into the seed coats [69]. It is assumed that CNTs regulate the aquaporins (AQPs) in the seed coats. The AQPs are membrane proteins and act as a water channel in the cell membrane.

Compared to the control condition, the TiO₂ (10 ppm concentration) on wheat displayed the lowest germination duration. In contrast, the shoot and seedling length was sufficiently higher at 2-10 ppm nanosized TiO₂ than that of the control [71]. However, higher TiO₂-based NP concentrations

had an inhibitory or no effect on wheat. Another research stated that the germination of aged spinach (*Spinacia oleracea*) seeds was accelerated by the nano-TiO₂ treatments at proper concentrations [72]. The *Cicer arietinum* showed that the application of nanorod hydroxylapatite (HAP) resulted in improved germination and increased growth of the plant. The better performance relative to control and other doses was found in the presence of 1 mg/mL Hap-nanorod [73]. Soybean seeds treated with super dispersive nanocrystalline powders of cobalt, iron, and copper in a zero-valent state under laboratory conditions showed increased germination frequencies relative to control conditions [74]. Data of the germination and growth impact of Ag NPs on 11 wetland plant plants, including *Eupatorium fistulosum*, *Panicum virgatum*, *Carex lurida*, *C. scoparia*, *Lolium multiflorum*, *C. vulpinoidea*, *C. crinita*, *Scirpus cyperinus*, *Phytolacca americana*, *Juncus effusus*, and *Lobelia cardinalis*, belonging to six distinct families has been shown to have differential responses to different species [75]. Accelerated seed germination was shown by the treatments of single-walled carbon nanohorns (SWCNHs) in six crop species: rice, barley, switchgrass, wheat, soybean, maize, tobacco, and tomato cell cultures [76].

3.3. Positive Impact of Nanoparticles on Plant Growth and Yield. In crop plant, the beneficial role of nanoparticles has been demonstrated: increased seed germination [77], increased shoot and root length [78], increased fruit production, improved metabolite content [79], and a substantial increase in seedling and plant vegetative biomass in many crops (Table 2). Similarly, the effect of nanoparticles has also been documented on several biochemical parameters related to plant growth and development, by increasing the nitrogen usage efficiency and enhancing the photosynthetic rate in several important crops plant, including peanuts [80], spinach [81–83], and soybeans [74]. Nanoparticles are also known for their role in improving the nutrient consumption and resistance of plants to various diseases and abiotic stresses [84]. NPs are capable of influencing plant growth and development by altering some of the physiological processes in plants. Most studies indicate that NPs can cause toxic effects above a certain concentration, and experiments based on plant toxicity evaluated their effect on the germination rate and biomass accumulation [85]. Some research has shown that NPs might also have significant effects on plants [86, 87].

The CNTs showed 100% germination in *Brassica juncea* and *Phaseolus mungo* at all concentrations and displayed a large increase in root length and amount of root hairs at 20 ppm, although a slight decrease in the number of root hairs was found at a higher concentration of 40 ppm [88]. In the seeds of *Cicer arietinum*, ZnO NPs improved the germination and growth rate [89]. In chickpea and mung at an optimal concentration of ZnO NPs, root and shoot growth improved while negative effects were observed after a certain concentration [90]. Low concentration (2 and 10 ppm) of TiO₂ NP has been shown to benefit wheat seedlings in terms of shoot lengths, higher TiO₂ NP concentrations have neutral effects, and TiO₂ bulk has inhibitory effects [91]. At a dose of

15 kg/ha of silica NPs, growth parameters such as several shoots and roots, stem height, stem diameter, leaf area, and root length of maize seedlings showed significant positive effects. In comparison, 20 kg/ha did not affect growth parameters [92]. Iron oxide (FeO) NPs are documented to promote the growth of wheat seedlings at a concentration of 100 ppm, while a high concentration of the same NPs decreased the rate of germination, root biomass, and mean time of germination [93].

Carbon dots (1.0 mg/mL) can play an important role in facilitating the growth of mung beans as they boost the beans' ability to consume and use nutrients more effectively [94]. The specific optical properties of carbon dots allow them to be transported by the vascular system through apoplastic pathways from the roots to the stems and leaves [94]. The calcium carbonate NPS accelerates growth parameters such as seed germination, root and shoot length, seedling vigor index, fresh and dry mass, and relative water content of mung (*Vigna mungo*) [95].

The positive effects of engineered nanomaterials (ENMs) on plants have also been identified as helping plants to consume more usable nutrients from fertilizers or soil water. For example, nano-ZnO in the mung bean rhizosphere has been confirmed to significantly increase the available form of P, soil microbial population, and root volume. This may be confirmed by the increased dehydrogenase activity, which is a measure of microbial activity and soil absorption of P by plants. The soil-developing microbes help maintain soil quality and structure for regular nutrient biogeochemical cycling [28]. In the plant cell, nano-ZnO is transformed into Zn₂₊ ions and regulates carbonic anhydrase activity for CO₂ fixation to carbohydrates. Zinc can be used as a cofactor for several enzymes, such as catalase and superoxide dismutase, to prevent oxidative damage to plant cells [28]. SiO₂ also increases the activity of nitrate reductase in combination with TiO₂ NPs. It acts as a key point in the reduction of nitrate (NO₃⁻) to nitrite (NO₂⁻) and improved plant absorption ability to improve fertilizer and water uptake [96]. The foliar application of ZnO NPs had a beneficial impact on tomato plant growth. It, therefore, opened up the question of the possible use of ZnO NPs as a future nanofertilizer. Likewise, foliar spray of ZnO NPs in pot-grown plants at 20 mg mL⁻¹ increases biomass production [97]. TiO₂ NPs have a beneficial effect on spinach growth by increasing the activity of Rubisco activase enzymes and enhancing the absorption of light or reducing the chloroplast oxidative stress caused by ultraviolet radiation during photosynthesis [98]. The anatase crystalline form of TiO₂ NPs exhibits the highest catalytic activity, facilitating chlorophyll and carotene synthesis in *Cucumis sativus* (*C. sativus*) [99]. Titanium dioxide enhanced the light absorption in chlorophyll-a molecules, oxygen evolution, and electron transfer rate in spinach leaves; TiO₂ NPs encourage chloroplast activity and Hill reaction [100].

The cerium (IV) oxide CeO₂ NPs increased stem elongation at 1–10 mg mL⁻¹, and a significant improvement in fruit weight was observed at 10 mg L⁻¹ [101]. Higher CeO₂ NP concentrations (500 mg kg per 1) culminated in rapid shoot development with increased biomass of 31% in barley. On

TABLE 2: The positive responses of nanomaterials on plant growth.

Nanomaterials	Concentration	Size (nm)	Effects on plants	Crops	References
CuO	500 mg kg ⁻¹ sand culture		Increased biomass	<i>Triticum aestivum</i>	[60]
SiO ₂	5 mM	4-10	Increased shoot biomass and grain weight	<i>Oryza sativa</i>	[104]
SWCNT	325, 1750 mg L ⁻¹	8	Increased the root length	Onion and cucumber	[105]
MWCNT	49 µg mL ⁻¹		Uptake nutrients (Zn, Mn, K, Ca, and Fe)	<i>Lycopersicon esculentum</i>	[106]
TiO ₂	0.01-0.05%	4-6	Enhanced growth, increased glutamate dehydrogenase, and glutamic pyruvic transaminase activity	Spinach	[107]
TiO ₂	300-1000 mg L ⁻¹	30	Inhibition of hydraulic conductivity	<i>Zea mays</i>	[108]
TiO ₂	1000 mg L ⁻¹		Chlorophyll content	<i>T. aestivum</i>	[109]
Activated carbon-based TiO ₂	0-500 mg L ⁻¹	30-50	Improved germination	Tomato	[110]
ZnO	20 ppm foliar spray	1.2-6.8	Increased biomass	Mung bean	[111]

the contrary, soil supplemented with low CeO₂ NP concentrations (125 and 250 mg kg⁻¹) stimulates grain production, whereas significant amounts of Ce are accumulated in grains and leaves. Besides, iron oxide NPs (IONPs) have been observed to increase the dry weight of soybean pods and leaves. IONPs have also been known as iron facilitators and aided in the transfer of iron photosynthate to peanut leaves, while IONPs increased root elongation in pumpkin, which is due to iron dissolution [96]. IONPs greatly encouraged tomato plant growth but caused green biomass to decrease [102]. The measurement of organic nitrogen in plant roots indicates that 51.1% of nitrogen (N) was present in roots relative to control [103], an indicator that TiO₂ NPs mediate the promotion of root growth by promoting N accumulation.

3.4. Positive Effects of Nanoparticles on Photosynthesis. Photosynthesis is the essential mechanism that converts light energy to chemical energy for plants on earth. All living things rely on photosynthesis either directly as their energy source or indirectly as their food's ultimate energy resource. In chloroplasts, the light source of energy is converted into a chemical form using chlorophyll, H₂O, and CO₂ as raw materials and stored in sugar molecule bonds. Several studies report that foliar application of metal NPs dramatically improves the content of chlorophyll in plants, enabling plants to synthesize more complexes for light harvesting to absorb more light energy and improve photosynthesis. TiO₂ is the most studied NP because it has a photocatalytic quality and can activate an oxidation-reduction reaction, contributing to the charge transfer between light-harvesting complexes II and TiO₂ NPs [112]. The effect of TiO₂ NPs on the photosynthetic efficiency of spinach has been reported, indicating that TiO₂ NPs can increase light absorption and accelerate light energy transport and transformation. Furthermore, due to the delay in the successful photosynthetic tenure of chloroplasts, TiO₂ NPs will prevent chloroplasts from aging. Nanoanatase TiO₂ enormously

improved the electron transport chain, O₂-evolving and photophosphorylation activity, and PSII photoreduction function of chlorophyll in spinach under both visible and ultraviolet (UV) radiation [113]. Also, the soluble protein and chlorophyll content of the ZnO NP-treated plants increased by 25% and 34.5%, respectively, compared to those of the control [114]. Chlorophyll content increased from 62.67 to 227.42% with an aerosol-foliar spray with rising concentrations of TiO₂ NPs up to 500 mg kg⁻¹. The transfer of TiO₂ NPs in soil induces a maximum increase in chlorophyll content of 216.29% at a concentration of 750 mg kg⁻¹ [54].

In *A. thaliana*, TiO₂ NP-treated plants have 3.83 times greater light-harvesting complex II (LHCII) content as compared to the control. The TiO₂ NPs improve the expression of LHCII b genes which play a key role in promoting chloroplast light absorption, regulating the distribution of light energy from photosystem I (PSI) to PSII by increasing the content of LHCII and accelerating the conversion of light energy to electronic energy, water photolysis, and oxygen evolution [115]. Zn is an essential plant micronutrient, whereas ZnO NPs have increased the content of chlorophyll in peanuts (1000 mg/kg) [80]. Specific ZnO NP concentrations have been found to boost the qualitative and quantitative characteristics of plants and to have higher PSII fluorescence kinetics (Phi-E0, Psi-E0, and PIABS) and lower energy flux parameter values (ABC/RC, TR0/RC, DI0/RC, and ET0/RC) [116]. In an in vitro model, manganese NPs are found to be involved in enhancing the photosynthetic electron transport rate and oxygen evolution [117]. Nanoiron, either alone or in combination with nanomagnesium, has been reported to have a major impact on chlorophyll's content [118]. In addition, the single-walled carbon nanotubes (SWCNTs) increased the rate of photosynthesis three times higher than the control by penetrating and accumulating in the lipid envelope of the extracted plant and increasing the rate of electron transport via a process consistent with amplified photoabsorption [119].

The rate of photosynthesis was significantly increased by SiO_2 NP treatments due to increased activity of carbonic anhydrase and photosynthetic pigment synthesis [120]. Treatment with ZnO NPs for 30 minutes (at 8 mg/L) has been reported to significantly increase the rate of photosynthesis and chlorophyll content, as well as increase the activity of carbonic anhydrase in tomato plants [121]. The increased rate of photosynthesis by nanoanatase TiO_2 in spinach was found to be due to the accelerated activity of Rubisco and Rubisco activase that enabled the carboxylation of Rubisco [122] (Figure 2). Rubisco activity has also been shown to be very sensitive to Ag NPs [123]. The treatments of iron sulfide NPs have been documented to enhance the growth and yield of the plant due to the activation of the Rubisco small subunit (*Rubisco S*) and Rubisco large subunit (*Rubisco L*) genes [124].

4. Role of Nanoparticles in Plant Stress Tolerance

Plants can adapt or cope with unfavorable conditions such as drought, salinity, chilling, and heat stress. Plant response to such abiotic stress is extensively studied at the cellular and molecular level [125]. A transitory provocation of cytoplasmic Ca^{2+} , ROS, abscisic acid, and increased mitogen-activated protein kinase (MAPK) pathways are included in the preliminary response of plants against abiotic stresses [126]. The advanced stage of stress response involves modulating proteins involved in cellular damage protection and regulating stress-specific gene expression.

Advances in nanomaterial engineering indicate that in existing adverse environments, nanofertilizers can improve the crop yield. In about 23% of the world's cultivated lands, salinity stress strongly limits crop production [127]. The SiO_2 NPs improve germination of seeds and increase plants' fresh and dry weight and chlorophyll content with proline accumulation under NaCl stress in tomatoes [128, 129]. The foliar spray of iron sulfate (FeSO_4) NPs exhibits a positive response in sunflower cultivars to salinity stress tolerance. The application of iron (II) sulfate (FeSO_4) NPs not only increased the leaf area, the net assimilation rate of carbon dioxide (CO_2), the chlorophyll content, the dry weight of the shoot, the substomatal concentration of CO_2 , the maximum photochemical efficiency of photosystem II (Fv/Fm), and the iron (Fe) content but also decreased the significant content of sodium (Na) in the leaves [21]. Titanium dioxide (TiO_2) nanoparticles were stimulatory to the expression of antioxidant enzymes in onion seedlings, and the activity of antioxidant enzymes was further increased when TiO_2 NPs were applied in combination with Ag NPs. The low TiO_2 concentration increased seed germination and onion seedling growth, while the effect was reversed at the higher concentration (suppressed). In addition to superoxide dismutase, which displayed concentration-dependent increases, hydrolysis enzyme (amylase), catalase, and peroxidase activity were significantly induced, while enzyme activity was higher at lower TiO_2 concentrations (10–30 $\mu\text{g}/\text{mL}$) and decreased at higher TiO_2 concentrations (40 and 50 $\mu\text{g}/\text{mL}$) [130]. The use of titanium nanoparticle foliar application on

wheat to mitigate the negative impact of drought stress has also demonstrated positive results for some agronomic characteristics such as starch and gluten. The findings indicated that the application of 0.02% TiO_2 nanoparticles showed improvement in different agronomic characteristics, i.e., plant height, ear number, ear weight, number of seeds, final yield, biomass, gluten-included harvest index, and drought stress starch content [131]. Silicon can potentially be used to alleviate to some degree the effects of drought stress. Previous studies found that exposure to low sodium silicate concentrations (1.0 mM) could moderately alleviate the adverse effects of wheat drought stress. Although the precise mechanism is unknown, silicon partially improves shoot growth, increases the content of leaf chlorophyll, and retains the capacity of leaf water in stressed plants. In addition, in wheat, it also decreases membrane lipid peroxidation [132].

It has also recently been investigated that silicon nanoparticles (SiNPs) can efficiently alleviate UV-B-induced wheat stress [22]. By controlling Cd accumulation, the foliar application of nano-Si at 2.5 mM concentration greatly increases Cd stress resistance in rice plants. Nano-Si fertilizers may seem to have an advantage over conventional fertilizers in reducing the accumulation of heavy metals [40, 133]. Despite various experiments on the stimulation of plant growth and stress resistance caused by nanomaterials, the underlying mechanisms remain largely uncovered [19]. The use of nanomaterials such as nano-ZnO or nano- SiO_2 improves the accumulation of free proline and amino acids, the absorption of water and nutrients, and the activity of antioxidant enzymes such as catalase, glutathione reductase, nitrate reductase, superoxide dismutase, and peroxidase, which improve the plant tolerance to the extreme conditions [134] (Figure 3). Furthermore, nanomaterials affect the expression of stress-related genes. For example, the application of Ag NPs in *Arabidopsis* microarray analysis shows that a variety of genes that play an important role in stress tolerance have been upregulated or downregulated [135]. The upregulated genes are a large part of the response to metals and oxidative stress (cation exchanger, superoxide dismutase, peroxidase, and cytochrome P450-dependent oxidase). In comparison, downregulated genes, including systemic acquired tolerance, ethylene signaling, and auxin-regulated genes implicated in growth and organ size, are linked to the response to pathogens and hormonal stimuli [136]. In plants, certain nanomaterial-induced responses are directly involved in defense against various environmental stresses. The response of plants to nanofertilizers depends on the plant species, their growth and development stages, and the type of nanoparticles [137]. Further study is required that this technology reaches the farm gate to identify signaling pathways and regulation of gene expression by specific nanomaterials in different plant species.

Farmers have been highly dependent on pesticides to minimize crop losses, negatively affecting the environment's sustainability and human health. Recent studies have shown that nanomaterials can effectively reduce the risks of pests and diseases, thereby reducing the incidence of yield losses and environmental risks. For example, the biosynthesized Ag NPs obtained from the *Gossypium hirsutum* stem extract

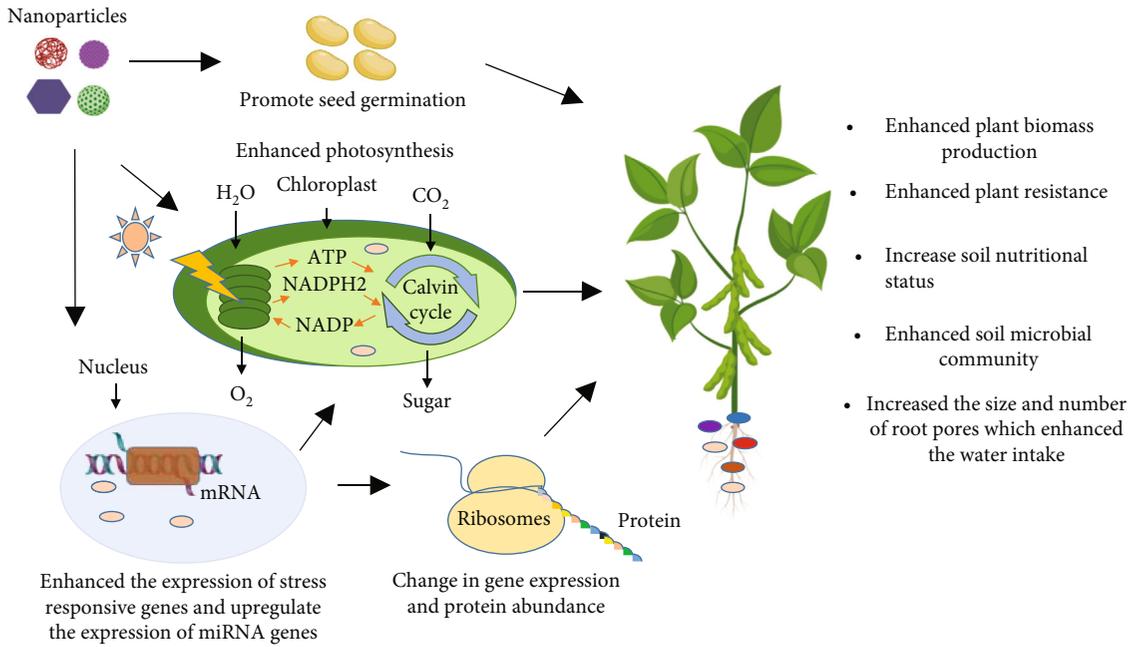


FIGURE 2: Positive effects of nanoparticles on plant growth and development. The optimum concentration of nanoparticles causes an alteration in different physiological processes to increase seed germination and photosynthesis of the plants. Further, the nanoparticles alter the gene expression of different genes and miRNAs that have a positive impact on stress tolerance and plant biomass.

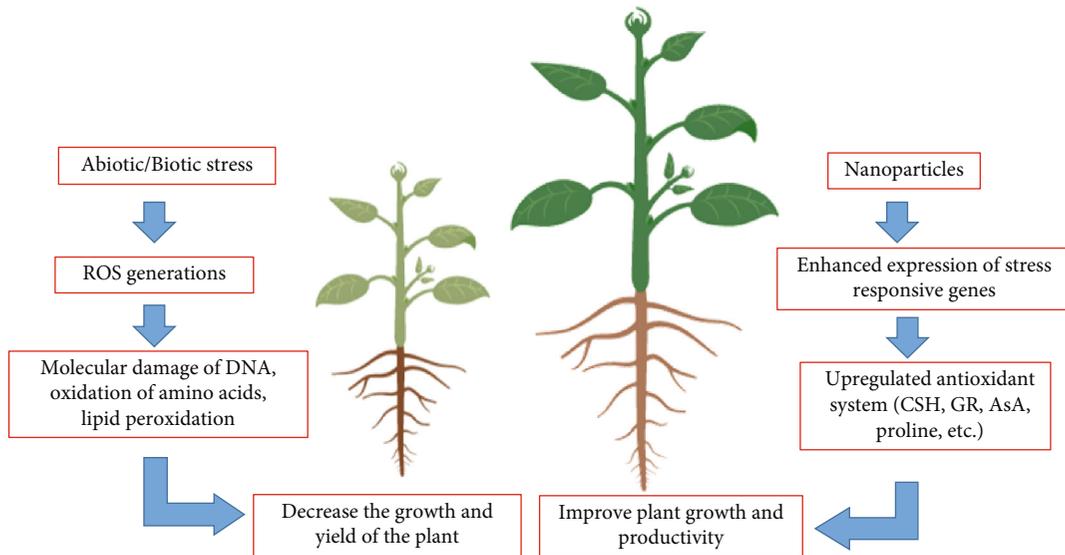


FIGURE 3: General mechanisms of nanoparticles increase the mitigating ability of plants under different stress environments.

have good antibacterial activity, as shown by the inhibition zone for *Xanthomonas campestris* pv. *campestris* and *Xanthomonas axonopodis* pv. *malvacearum*, two of the Malvaceae and Brassicaceae family's largest bacterial pathogens [138]. The metal oxides ZnO, CuO, and MgO could also effectively regulate many plants and soil-borne pathogen such as *Alternaria alternata*, *Botrytis cinerea*, *Colletotrichum gloeosporioides*, *Fusarium solani*, *Monilinia fructicola*, *Fusarium oxysporum* f.sp. *radicis lycopersici*, *Ralstonia solanacearum*, *Verticillium Dahliae*, and *Phytophthora infestans* in different plant species [139–142]. The use of the fungicide

Antracol with Ag-incorporated nanocomposites (Ag@CS) has improved antifungal efficacy relative to being used alone [19].

By reducing plant membrane disruption and ion leakage, TiO₂ nanoparticles maintain the ability to decrease the negative impact of chilling tension. Photosynthesis is the plant system's integral process that is very sensitive to chilling stress [143]. The chilling stress damages the plant photosystem, reduces the chlorophyll content, absorption of CO₂, and transpiration rate, and degrades the photosystem enzyme (Rubisco) [115]. The effect of nanoparticles on the

photosystem has been achieved by increasing Rubisco enzyme production and chloroplast light immersion capacity [115] and inhibiting ROS production [119]. Exposure to TiO₂ nanoparticles increases the expression of the Rubisco and chlorophyll-binding protein gene [144], leaf pigments, and antioxidant enzyme activities [145] and improves resistance to stress chilling. Plants suffering from cold stress upregulated the genes MeAPX₂ and MeCu/ZnSOD and increased the activities of dehydroascorbate reductase, monodehydroascorbate reductase, and glutathione reductase that scavenge ROS, resulting in repressed oxidative stress, i.e., lipid peroxidation, degradation of chlorophyll, and production of H₂O₂, eventually ensuring stress tolerance [146]. However, increased growth and biochemical physiognomies of plants exposed to cold stress have been shown by nanoparticle exposure along with chilling stress. The low concentration of selenium (Se) nanoparticles decreased the impact of heat stress by improving the chlorophyll content, hydration ability, and plant growth [147]. The low concentration of Se nanoparticles shows plant antioxidant activities, while oxidative stress is caused by the high concentration of Se nanoparticles [148]. Plants also synthesized several heat shock proteins and molecular chaperones during heat stress. Heat shock proteins help other proteins in maintaining their constancy in stress environments and are involved in heat stress tolerance [149]. Multiwall carbon nanotubes have been documented to be involved in upregulating gene expression of heat shock proteins, such as HSP90 [150].

4.1. Molecular Mechanism of Nanoparticles to Mitigate Environmental Stresses. Plants are influenced by different environmental stresses during their life cycle and thus improve their defense against environmental stress at different stages by modulating genetic, biochemical, and physiological pathways. Plants adopt molecular routes by sufficient modification of gene expressions to cope with these stresses. Several studies have shown that the induced impact of nanoparticles on plant growth and development depends on their concentration. In plants, the signaling network stimulates the defensive system, which triggers the molecular mechanism to respond to specific stress conditions. Calcium ions involved in the transduction of signals under varying stress environments act as a second messenger [151]. Sensitivity to stress signals causes the enrichment of calcium ion level in the cytosol through calcium ion channels, which is recognized by calcium ion-binding proteins that trigger alterations in gene expression as well as plant adaptation to stress conditions [152, 153]. Nitric oxide (NO) has been shown to cause the enhancement of cytosolic calcium ions in plant cells under various biotic and abiotic stress conditions [152, 153], and thus, calcium ions persuade the synthesis of nitric oxide [154]. In *O. sativa*, the Ag nanoparticle treatment on roots showed that the nanoparticles were involved in responsive protein regulation and signaling of calcium ions, transcription, protein degradation, oxidative stress response pathways, cell wall synthesis, and cell division [155]. Ag nanoparticles are also documented to bind to calcium ion channels or Ca_v1/Na_v1 ion pumps through calcium ion receptors that influence cell metabolism. Besides, the association

of C60 nanocrystals induced the functional regulation of Ca_v1/calmodulin-dependent protein kinase II [156]. In addition, cadmium sulfide QDs induced overexpression of calcium-binding protein CML45 and calcium-dependent protein kinase 23 in *A. thaliana*. These calcium-binding proteins have been shown to regulate stress responses, and their overexpression increased plant tolerance to many abiotic stress conditions [157]. The stimulation of calcium ions by nanoparticles revealed that nanoparticles impersonate calcium ions and bind to calcium-binding proteins that activate the cascade of genes that respond to stress [158].

The exposure to zero-valent iron nanoparticles in *A. thaliana* upregulated the gene expression of *AHA2*, which is involved in stomatal opening and enhanced the tolerance of drought [159]. In *A. thaliana*, the gene expression analysis of RT-PCR and the whole-genome microarrays of cDNA expression provided new insights into the molecular mechanisms of plant responses to Ag NPs [160]. Analysis of the whole-genome cDNA microarray revealed upregulation of 286 genes, including genes mainly associated with metal and oxidative stress (e.g., cytochrome P450-dependent oxidase, vacuolar cation/proton exchanger, peroxidase superoxide, and dismutase), and downregulation of 81 genes, including plant defense and hormone stimulus genes [155]. In *A. thaliana*, the effect of zinc oxide (ZnO) [161], fullerene soot (FS), or titanium dioxide (nTiO₂) nanoparticles on root gene expression showed 660 up- and 826 downregulated genes, 232 up- and 189 downregulated genes, and 80 up- and 74 downregulated genes, respectively (translation gap > 2-fold). The ZnO and FS mediated genes predominantly ontological groups annotated as stress responsive, including abiotic responsive genes such as drought and salinity as well as biotic genes including pathogen defense and wounding stimuli [69].

The miRNAs have been involved in the control of plant and animal biological processes and play an important role in plant responses to abiotic and biotic stresses [162]. In *A. thaliana* and *N. tabacum*, the microRNA (miRNA) gene expression was analyzed. The microRNAs are small noncoding RNAs (22–24 nucleotides), which regulate the posttranscriptional gene expression by inhibiting mRNA translation to peptides or degrading mRNA [163]. The miRNAs have been reported to mediate the stress-responsive gene expression during salt and water stress by modifying gene expression. In a tobacco cell, the nanotube stimulates the growth and gene expression [164]. It has been reported that miRNA genes are upregulated and played an important role under Al₂O₃ NP stress. With increasing concentrations of Al₂O₃ NPs, the expression of nine miRNAs (miR159, miR162, miR167, miR169, miR395, miR396, miR397, miR398, and miR399) was significantly upregulated [162, 163].

5. Nanomaterials for Genetic Engineering

Climate change and an increasing world population and genetic modification of plants have improved crop production by conferring desirable genetic traits to crops. The plant cell walls act as a barrier in the delivery of exogenous molecules into plant cells. Various strategies based on

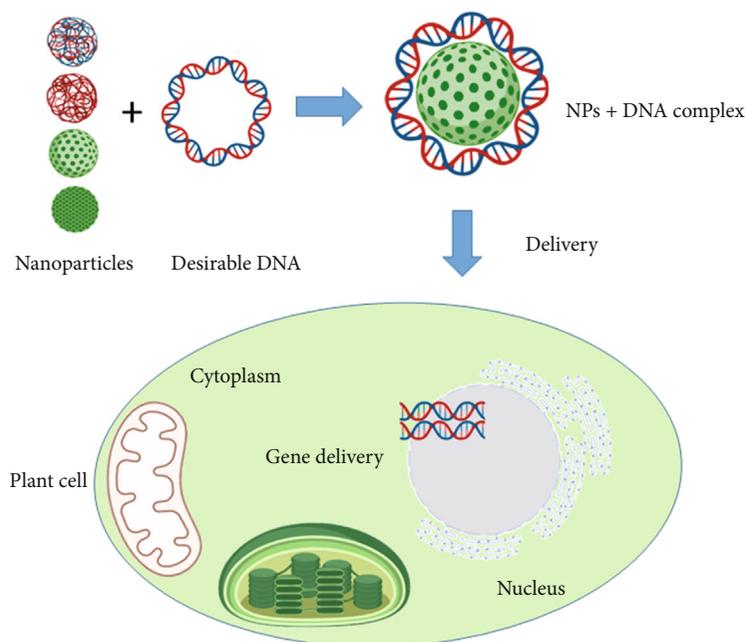


FIGURE 4: Graphical presentation of nanomaterials acting as a substitute of conventional gene delivery systems for plant genetic engineering.

Agrobacterium transformation or biolistic approaches are used worldwide for DNA transmission in plant cells to conquer this challenge and achieve plant genetic transformation. Limitations to these techniques are based on limited host range and extensive damage to plants, often preventing the plant development. Genetic engineering, although there is advancement in plants, has lagged and recently seen significant advancements. There are relatively fewer plants than the various and complex gene and protein distribution methods developed for animal systems. In general, modern plant genetic transformation requires two main steps: the distribution of genetic delivery and regeneration of the transformed plant, the requirement and complexity of the latter being strongly dependent on what method of delivery is used and how much the transformation is stable. There are three components of regeneration procedures: the induction of competent totipotent tissue, callus-forming tissue culture, and selection and progeny segregation.

Several of the pioneering experiments in nanomaterial-based plant genetic engineering have been carried out in plant cell cultures. Nanoparticles are attractive materials for biomolecule transmission due to their ability to penetrate plant cell walls without external force, wide host range applicability, and highly tunable physicochemical properties.

For instance, a good approach to delivering DNA in different calli (maize, soybean, tobacco, rice, and cotton) has been documented as silicon carbide-mediated transformation [165, 166]. Although lagging behind the progress made in animal systems, findings recently published in plants suggest that NMs can transcend the cell wall barrier in adult plants and reduce the limitations of current transgene delivery systems. One seminal study showed that dsRNA of various plant viruses could be loaded on nontoxic, degradable, layered double hydroxide (LDH) clay nanoparticles or

BioClay. The dsRNAs and/or their RNA breakdown products offer protection in sprayed tobacco leaves against the Cauliflower Mosaic Virus (CMV), but they also confer systemic protection of the viral challenge to newly emerged, unsprayed leaves 20 days after a single tobacco spray procedure [167]. An effective, stable genetic transformation via magnetic nanoparticles (MNPs) has been achieved in cotton plants. The β -glucuronidase (GUS) reporter gene-MNP complex has been magnetically infiltrated into cotton pollen grains without affecting the pollen's viability. Cotton transgenic plants were successfully produced by pollination with magnetofected pollen, and exogenous DNA was successfully incorporated into the genome, effectively expressed, and stably inherited in the self-acquired offspring [168]. The scaffolds of carbon nanotubes applied by infusion to external plant tissue were used to transfer linear and plasmid DNA and siRNA into *E. sativa* protoplasts and *T. aestivum*, *Gossypium hirsutum*, *Eruca sativa*, and *Nicotiana benthamiana* leaves resulting in a high transient expression of Green Fluorescent Protein (GFP). The small interfering RNA (siRNA) was additionally supplied to *N. Benthamiana* plants that constitutively expressed GFP, allowing the gene to be silenced by 95% [169]. The first and most promising approach to mesoporous silica nanoparticle- (MSN-) mediated genome editing has recently been proposed. MSNs are used as carriers in *Zea mays* immature embryos to transport Cre recombinase, carrying loxP sites incorporated into chromosomal DNA. The loxP was correctly recombined after the biolistic application of engineered MSNs in plant tissues, establishing an effective genome editing [170]. As such, NP-based biomolecule delivery to plants is designed to allow DNA, single guide RNA (sgRNA), and RNP delivery for higher-throughput plant genome editing (Figure 4). Thus, it warrants a discussion on the state of the plant genome editing field.

6. Conclusion and Perspectives

In recent years, nanotechnology research has suggested the development of NPs as a powerful technique to reduce existing problems resulting from conventional fertilizers in traditional agricultural systems. The results relating to nutritional elements containing NPs (i.e., Fe, Cu, Se, and Co) have shown substantial scientific evidence of their efficacy in improving the micronutrients of the plant, which has been reflected by improved growth parameters and significant improvements at the physiological level (i.e., chlorophyll and carotenoids, photosynthetic activity, metabolic pathways, and transpiration rate). A major obstacle is the precise dosage and activity of NPs on the surface of plant targets, so minimizing the leakage of chemical products extracted from bulk materials (i.e., mineral fertilizers) has become a valuable feature that facilitates the future use of NPs. However, critical studies carried out under controlled conditions are desperately required to determine the role of NPs in and out of the plant and their effects on the environment. The basic dosage of NPs, exposure duration, translocation and accumulation, and mechanism of action on plants are important for an application strategy to be developed. In addition, the secondary effects and accumulation of soil, air, water, and biotic organisms in the ecosystem are critical in deciding the exact impacts of NPs and their effects on the ecosystem.

Data Availability

All data generated or analyzed during this study are included in this published article.

Conflicts of Interest

The authors declare no conflict of interest.

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