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REVIEW ARTICLE

Nano-enabled stress-smart agriculture: Can nanotechnology deliver drought and salinity-smart crops?

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Abstract

Salinity and drought stress substantially decrease crop yield and superiority, directly threatening the food supply needed to meet the rising food needs of the growing total population. Nanotechnology is a step towards improving agricultural output and stress tolerance by improving the efficacy of inputs in agriculture via targeted delivery, controlled release, and enhanced solubility and adhesion while also reducing significant damage. The direct application of nanoparticles (NPs)/nanomaterials can boost the performance and effectiveness of physio-biochemical and molecular mechanisms in plants under stress conditions, leading to advanced stress tolerance. Therefore, we presented the effects and plant responses to stress conditions, and also explored the potential of nanomaterials for improving agricultural systems, and discussed the advantages of applying NPs at various developmental stages to alleviate the negative effects of salinity and drought stress. Moreover, we feature the recent innovations in state-of-the-art nanobiotechnology, specifically NP-mediated genome editing via CRISPR/Cas system, to develop stress-smart crops. However, further investigations are needed to unravel the role of nanobiotechnology in addressing climate change challenges in modern agricultural systems. We propose that combining nanobiotechnology, genome editing and speed breeding techniques could enable the designing of climate-smart cultivars (particularly bred or genetically modified plant varieties) to meet the food security needs of the rising world population.

KEYWORDS

abiotic stress, engineered nanoparticles, genome editing, nanobiotechnology, speed breeding

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1 | INTRODUCTION

Nanotechnology is an interdisciplinary area that has emerged as a growing industry introducing engineered nanoparticles (NPs) into the global market with the potential to advance agricultural science and other related sectors (Khan et al., 2017; Usman et al., 2020; Vithanage et al., 2023). In recent years, agricultural practices have incorporated products (derived from in-house R&D and patented technologies and processes) containing engineered NPs such as NPs, nanomaterials, nanocapsules, nanocarriers, nanofertilizers, nanopesticides and nanosensors to enhance their sustainability and productivity (Dziergowska & Michalak, 2022; Usman et al., 2020). Nanoscale matter exhibits various properties that differ from its bulk matter counterpart, so as these novel properties are chartered and evaluated, these nanostructures can be used in various fields. Nanotechnology has four significant applications in agriculture: (i) stimulating plant growth, (ii) increasing crop productivity, (iii) improving soil quality and (iv) smart monitoring (Dziergowska & Michalak, 2022). Nanotechnology creates and tests the use of specialised particles (1–100 nm in size) administered as NPs (Khan et al., 2017). The small size, shape and surface area of these particles amplify their adsorption to cellular locations and target the delivery of beneficial substances (Dziergowska & Michalak, 2022; Usman et al., 2020). The utilisation of NPs in the agricultural sector is gaining momentum due to their desired role in augmenting crop growth, soil health and crop productivity (Landa 2021). In recent years, different rare earth metal-based NPs, such as zinc oxide NPs (ZnO-NPs), zinc NPs (Zn-NPs), silver NPs (Ag-NPs), iron sulphide NPs (FeS_2-NPs), iron NPs (Fe-NPs), cerium oxide NPs (CeO_2-NPs), silica NPs (SiO_2-NPs), gold NPs (Au-NPs), titanium dioxide NPs (TiO_2-NPs), copper oxide NPs (CuO-NPs) and carbon-based NPs (e.g., carbon nanotubes and fullerols), have been administered in controlled and natural field conditions to enable plants to survive in various stressed environments (Usman et al., 2020; Zahedi et al., 2019; Zulfiqar & Ashraf, 2021). Studies have demonstrated that NPs can negatively and positively alter plant growth depending on the size and dose used (Chen et al., 2015; Singh, Tiwari, et al., 2021).

Nanotechnology is still revolutionising the agricultural field due to the vast array of nanomaterials that enhance food and crop production (Tighe-Neira et al., 2022; Vithanage et al., 2023; Yang, Yuan, et al., 2021). Exogenous application (foliar or soil) of NPs in agriculture has appeared as a hopeful technique for improving crop development and productivity under normal and stressed conditions (Rashid et al., 2017; Yusefi-Tanha et al., 2020). Moreover, NPs can enter the root epidermis or aerial surface through apoplastic and symplastic pathways (Pullagurala et al., 2018). Nanoparticle movement inside plant parts is active or passive, with their uptake and transport dependent on their size (Arshad et al., 2021). Recent investigations suggest that NPs contribute to different physio-biochemical processes regulating plant growth, productivity and responses to harsh abiotic stresses (Hussain et al., 2018; Usman et al., 2020). Moreover, the exogenous application of NPs can increase specific morpho-physiological processes, including seed germination, plant height, fresh dry weight, flower count, fruit yield, early flowering and overall crop yield (Ali et al., 2021). Beneficial NPs can be used as nutrient or fertiliser nanocarriers, resulting in increased efficiency and reduced environmental contamination than traditional fertilisers due to their physio-chemical properties and modes of action (Gohari, Zareei, et al., 2021; Landa, 2021).

However, plants are sessile organisms that cannot evade harsh environmental cues, including salinity, drought, temperature and flooding that reduce crop yields (Ding & Yang, 2022; Raza, Mubarik, et al., 2023; Rivero et al., 2022; Zandalinas et al., 2021). The increase in salinity and drought stress episodes caused by global climate change events has decreased crop growth and threatened food security (Farooq et al., 2022; Kumar et al., 2021; Rivero et al., 2022; Wang et al., 2021). Salinity stress, a mixture of osmotic and ionic stress, arises from unpropitious salt buildup in soil (Alam et al., 2021; Gupta et al., 2021; Melino & Tester, 2023), which decreases plant health by adversely affecting cellular processes due to ionic cytotoxicity caused by the accumulation and exchange of mineral ions with Na^+ (Johnson & Puthur, 2021; Melino & Tester, 2023; Raza et al., 2022). Drought is a complex abiotic stress caused by low rainfall and extreme temperatures, which alter plant characteristics and development processes (Bhardwaj & Kapoor, 2021; Laxa et al., 2019). It is frequent in arid and semiarid areas, disrupting plant processes, especially transpiration rate, stomatal conductance, photosynthetic frequency, water potential and leaf relative water content (RWC), at all stages of plant growth (Hammond et al., 2022; Lamaoui et al., 2018; Raza, Mubarik, et al., 2023; Yang & Qin, 2023). Drought stress can also disrupt cell division and meiosis, diminish pollen grains, cause pollen sterility and lead to plant necrosis (Fahad et al., 2017). Salinity and drought stress can also trigger the overgeneration of reactive oxygen species (ROS) by disrupting a plant's internal defence system (Hasanuzzaman et al., 2020; Mittler et al., 2022), causing oxidative stress that damages cellular organelles (DNA, lipids and protein), enzymatic arrangement and eventually triggers cell death (Abbas et al., 2020; Mittler et al., 2022; Singh, Tiwari, et al., 2021).

Thus, identifying modern technologies and methods to develop drought and salinity tolerant/resilient plants (hereafter termed 'stress-smart plants') is important for future global food security and modern agriculture's resilience, efficiency and progress. Hence, we reviewed the application of nanotechnology (mainly NPs) in the cultivated field to explore its potential and how it can improve crop health and overall productivity, especially under drought and salinity stresses, to help future-proof agricultural practices against current and emerging global climatic challenges. We also uncover the scope of NP-induced gene editing to fast-track crop innovations under stressful conditions.

2 | EFFECTS AND RESPONSES OF PLANTS TO STRESS CONDITIONS

2.1 | Salinity stress

Plants have natural adaptation mechanisms to manage diverse environmental stresses and are categorised as glycophytes or

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halophytes, depending on their ability to grow and persist under salinity (Liu et al., 2020). In response to salinity stress, plants exhibit short- or long-term morphological, physiological, biochemical, molecular and cellular levels to maintain growth and production (Melino & Tester, 2023; Raza et al., 2022). The short-term response involves encountering stress through the root system by a sharp reduction in soil water potential, causing osmotic stress. In the long term, ionic toxicity is induced due to the over-accumulation of salts in the cytoplasm, and vacuoles can no longer remove the excessive salt (Baetz et al., 2016; Melino & Tester, 2023). Sodicity also induces higher ion uptake and increases rhizosphere pH due to carbonates and bicarbonates that hinder nutrient uptake. Under salinity, root growth is drastically reduced and shoot growth is stunted (Mujeeb-Kazi et al., 2019; Zörb et al., 2019). In addition, osmotic stress adversely affects cell functions, water status repositioning and membrane stabilisation (Liu et al., 2020; Melino & Tester, 2023; Mujeeb-Kazi et al., 2019; Zörb et al., 2019). Leaf tip burning is a peculiar symptom of salinity (Singh et al., 2009), with significant leaf senescence and ion homoeostasis noted in *Brassica juncea* (Alamri et al., 2020).

Plants regulate cell wall elasticity, adjust osmotically and increase apoplastic water percentage under salinity stress (Hernández 2019; Melino & Tester, 2023; Saddiq et al., 2021). Osmotic adjustment is regulated through the accumulation of several compounds, mostly organic sugars (e.g., sucrose, sorbitol, mannitol, glycerol, raffinose, arabinitol, pinitol and galactinol) (Filippou et al., 2021; Patel et al., 2020), nitrogen-containing compounds, for example, proteins, glutamate, aspartate, glycine betaine (Zhang, Lei, et al., 2018), proline, choline, polyamines, four-gamma aminobutiric acid (Antoniou et al., 2021; Ashraf et al., 2018; Patel et al., 2020) and organic acids like malate and oxalate (Fang et al., 2021; Patel et al., 2017). Proline and glycine betaine are well-reported compatible solutes for their role in osmotic regulation in plants against salinity stress (Antoniou et al., 2021; Khalid et al., 2020; Patel et al., 2017). Proline also has antioxidant properties, with salt-tolerant plants storing/accumulating proline for reoccurring stresses (Hernández, 2019; Saddiq et al., 2021). In contrast, glycine betaine work as an osmolyte molecule to protect photosystem II (PSII) (Huang et al., 2020). The harshness of stress and age of the plant are additional determinants of osmotic adjustments. Chloroplast ultrastructure and starch content also change under salt stress, suggesting that starch is imperative for maintaining several physiological processes in plants (Chen et al., 2008; Goussi et al., 2018). Root density also increases the preservation of toxic ions in the root zone of salt-tolerant species (Julkowska et al., 2017).

Phytohormones regulate physiological, biochemical and molecular mechanisms under salt stress (Fahad et al., 2015). At the molecular level, this response involves regulating the genes expression accountable for phytohormone biosynthesis (Fahad et al., 2015; Raza, Charagh, et al., 2023; Wani et al., 2016). Different proteins are expressed under salinity—induced by these phytohormones—and their endogenous levels help determine the mechanism of plant stress tolerance (Wani et al., 2016). The stress hormone, abscisic acid (ABA), plays a vital role at the molecular level in regulating the expression of salt-responsive genes (Jiang, Tong, et al., 2021; Vishwakarma et al., 2017) and maintaining osmotic balance by mediating guard cell movement in plants (Devinar et al., 2013). ABA also contributes to the production and accumulation of osmoprotectants (e.g., proline) and the expression of stress-receptive proteins (dehydrins and late embryogenesis abundant proteins) (Cheng et al., 2018). ABA-mediated accumulation of hydrogen peroxide (H_2O_2) in cells results in the generation of nitric oxide, leading to the expression of mitogen-activated protein kinase and antioxidative enzymes to scavenge ROS (Fahad et al., 2015; Kaur & Bhatla, 2016). Additionally, auxin (IAA) plays a dynamic part in stress-mediated signal transduction and seed germination under salt stress (Korver et al., 2018), while cytokinins mediate oxidative stress via proline synthesis and induce salinity tolerance in plants. Cytokinins are also important in vascular and shoot discrimination, anthocyanin creation and photo-morphogenic advancement in plants under salt stress (Gengmao et al., 2015). Gibberellic acid is responsible for various metabolic processes, regulating the sugar signalling pathway and different antioxidant activities. Moreover, gibberellic acid enhances ribonuclease and polyphenol oxidase events under salt stress (Camara et al., 2018; Jain et al., 2012). Ethylene-mediated leaf abscission also helps minimise transpirational water losses (Zhang et al., 2016). Other phytohormones, including salicylic acid, brassinosteroids, jasmonates, and triazoles, have been reported to counteract salinity at a physiological and molecular level (Fahad et al., 2015).

Salt stress induces various morphological and anatomical modifications in plants, including reduced total leaf area and leaf growth, increased leaf thickness and palisade parenchyma, and increased intercellular spaces due to a reduction in spongy parenchyma (Acosta-Motos et al., 2017), facilitating carbon dioxide (CO_2) diffusion under stomatal limitations (Zhu et al., 2018). Stomatal closure promotes tissue respiration and decreases carbon integration in the short term, decreasing the photosynthesis rate in salt-tolerant species (Li et al., 2020; Zhang, Kaiser, et al., 2018). Severe salt stress can also cause photo-inhibition or increased mesophyll resistance, resulting in primarily irreparable impairment to plants or, in some cases, delayed recovery after removal of the stress (Kibria et al., 2017; Li et al., 2020; Zhang, Kaiser, et al., 2018). In the long term, salt stress decreases net CO_2 assimilation to a minimal level, closing stomata to a maximum level and decreasing chlorophyll (Chl) content and photosynthetic activity (Alamri et al., 2020; Li et al., 2020; Zhang, Kaiser, et al., 2018). Plants respond by maintaining/increasing their photosynthetic pigment content and photo-chemical quenching parameters, resulting in stunted growth (Porcel et al., 2015). Plant photosynthetic activity is also disturbed by oxidative stress at the subcellular level, increasing lipid peroxidation and protein oxidation (Chaves et al., 2009; Yang et al., 2020).

Furthermore, photo-inhibition of PSII increases ROS production (Choudhury et al., 2017; Hasanuzzaman et al., 2020; Mittler et al., 2022). In response, plants produce enzymatic antioxidants, such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbic acid peroxidase (APX) and glutamate reductase, which

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scavenge ROS to defend against oxidative stress (Hasanuzzaman et al., 2020; Mittler et al., 2022). The activation and upregulation of enzymatic antioxidative activities are considered some of the best salt-responsive mechanisms in tolerant plants (Kibria et al., 2017). Xanthophyll cycle activity also increases to dissipate excessive amounts of energy during PSII through a nonphoto-chemical quenching process (Wu et al., 2018; Zheng et al., 2019), and photorespiration and the water–water cycle act as responsive mechanisms to inhibit the reduction of photosynthetic electron chain and protect the photosynthetic machinery from ROS by dissipating excess amounts of photon energy from the system (Haber et al., 2021; Voss et al., 2013). Salt elimination from the cytoplasm, assortment in vacuoles, and reduced hydraulic conduction of membranes via aquaporins, which manipulate water transfer beyond the soil–plant systems, are also defensive reactions of plants against salinity stress (Jia et al., 2020; Singh et al., 2020).

2.2 | Drought stress

Climate change has increased drought stress episodes, posing a substantial risk to world food safety by lowering crop growth (Narayanasamy et al., 2023; Raza, Mubarik, et al., 2023). Droughts are responsible for about 50% of annual crop yield losses, and in several territories of the planet, the duration and occurrence of drought stress are projected to enhance, leading to severe crop yield losses (Rasheed et al., 2023; Raza, Mubarik, et al., 2023; Varshney et al., 2021; Wang et al., 2023; Zhao et al., 2023). Plant responses to drought stress are reliant on several features, including the period and strength of the stress, the genetic makeup of the plant and the developmental period (Salvi et al., 2021; Varshney et al., 2021). The consequences of drought stress on plants are widespread, impacting all stages of plant growth, soil heterogeneity and nutrient mobility and access (Limousin et al., 2022; Raza, Mubarik, et al., 2023; Riyazuddin et al., 2022; Yang & Qin, 2023). Water deficiency can result in decreased vegetative growth and biomass, which are associated with key developmental switches such as the reproductive transition (Cooper & Messina, 2023; Wang et al., 2023). Furthermore, drought stress can alter the plant's carbon metabolism by repressing key biochemical and photochemical processes, including Rubisco inactivation, slow RuBP regeneration and stomatal closure, which result in limited CO_2 diffusion into the leaves (Pandey et al., 2023; Yang & Qin, 2023).

Drought stress also impacts the photosynthesis pigment-protein complex, reducing PSII efficiency and the quantum yield of PSII electron transport chain (Gholami et al., 2022; Raza, Mubarik, et al., 2023; Yang & Qin, 2023). As a result, drought primarily hinders the photosynthetic process, reducing plant height, biomass and early senescence. Moreover, drought stress upregulates the alternative oxidase pathway and triggers the activity of nicotinamide adenine dinucleotide-malate dehydrogenase and nicotinamide adenine dinucleotide phosphate-malate dehydrogenase (Ahmad Lone et al., 2022). Furthermore, drought stress frequently disrupts RWC in plants leading to oxidative and osmotic stress resulting in ionic inequity and severe injury to cell membranes and other in *planta* cellular functions (Asghar et al., 2022; Cooper & Messina, 2023). Gradual exposure to drought stress triggers ROS generation, including hydroxyl radical, singlet oxygen, superoxide anion free radical and H_2O_2, which increase lipid peroxidation, interfering with cellular metabolism by being detrimental to the functionality of proteins, lipids and macromolecules (Ayyaz et al., 2021; Pandey et al., 2022; Raza, Mubarik, et al., 2023). Drought stress limits nutrient movement by mass flow and diffusion in soil and restricts their uptake into the vascular system and aerial plant parts (Plett et al., 2020). Several indirect consequences of drought stress on overall crop yield and development have been described (Cooper & Messina, 2023; Liu et al., 2022; Rasheed et al., 2023; Raza, Mubarik, et al., 2023; Yang & Qin, 2023). Recent literature indicates that drought stress disrupts the functioning of numerous physiological processes throughout a plant's life cycle, that is, flowering time, leading to pollen grain sterility, functions of reproductive organs and limiting final crop yield (Cooper & Messina, 2023; Wang et al., 2023; Wu et al., 2022; Yang, Lu, et al., 2021).

Plants need adequate water for their survival, development and reproduction, and when faced with water deficiency, they exhibit various response strategies to maintain a higher water potential (Abbas et al., 2023; Cooper & Messina, 2023). Different plant species manifest different approaches to manage drought stress, such as an accelerated life cycle before drought onset, the ability to store and retain higher water content through drought (Du, Zhao, Chen, Yao, Zhang, et al., 2020), fluctuating root hydraulic conductance, enhanced aquaporin expression and synthesis of dehydrins stress proteins (Gharibi et al., 2019; Tiwari et al., 2021). Plants store osmoprotectants and osmolytes to protect their proteins and membranes under the denaturing effect of drought conditions (Gilbert & Medina, 2016). Plants also increase their osmotic potential at the cellular levels by accumulating osmolytes, such as proteins, soluble carbohydrates, free amino acids, proline and glycine betaine (Kausar, Zahra, et al., 2023; Salvi et al., 2021).

Under drought conditions, plants demonstrate plasticity feedback by off-putting the extreme transpiration rate, leading to higher transpiration efficiency and water saving in plants (Bacher et al., 2022; Salvi et al., 2021). Plants also enhance the creation of secondary metabolites, such as flavonoids help with drought acclimation by regulating heat shock factors and chaperones (Baozhu et al., 2022). Plants also remobilise carbohydrate metabolism via source–sink associations to tolerate drought and accelerate recovery to decrease yield fluctuations (Correia et al., 2022). Furthermore, several plant polyphenols with ROS quenching ability, such as anthocyanins, caffeic acid, 4-coumaric acid, ferulic acid, catechin, cis-resveratrol-3-*O*-glucoside, rutin, quecetin and quecetin-3-*O*-glucoside, kaemoferol and kaempferol-3-*O*-glucoside, apigenin and chlorogenic acid, have been found receptive to drought stress (Sharma et al., 2019; Takahashi et al., 2021).

In response to drought stress, plants initiate numerous complex signalling ways that trigger antioxidant defence and phytohormone-facilitated signalling (Álvarez-Aragón et al., 2023). Evidence suggests that plants stimulate antioxidant defences such as POD, SOD, CAT and APX to scavenge ROS and withstand stress

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(Choudhury et al., 2017; Mittler, 2002; Mittler et al., 2022; Raza, Mubarik, et al., 2023). Plant reactions to drought stress are also directed by a system of signalling pathways that perform a key role in plant adaptation to drought stress, including different phytohormones, that is, ABA, cytokinin, auxin, salicylic acid, brassinosteroids, jasmonates and ethylene (Abbas et al., 2020; Mubarik et al., 2021; Raza, Mubarik, et al., 2023). In particular, ABA is an important stress-responsive hormone and a key regulator in plant adaptation to drought stress (Mubarik et al., 2021). Drought stress perception induces ABA biosynthesis in plants, regulating stomatal aperture, slowing water loss through transpiration, and activating ABA response genes to prevent dehydration (Li, Yang, et al., 2021; Saradadevi et al., 2017; Takahashi et al., 2020). Recent reports have also suggested that novel hormones like peptides act as active molecules in the plant vasculature under drought stress, triggering water deficit indicators in long-distance tissue-to-tissue interaction to integrate drought responses (Saradadevi et al., 2017; Takahashi et al., 2019).

Plants have evolved numerous molecular responses to drought stress by modulating gene expression (Raza, Mubarik, et al., 2023; Wang et al., 2023). Different genes respond to water deficit conditions at the transcriptional level (Raza, Mubarik, et al., 2023; Wang et al., 2023; Yang & Qin, 2023). For example, expression of the *CarMT* gene under drought stress enhanced the antioxidative system, increasing the drought tolerance of Arabidopsis plants (Dubey et al., 2019), while the *ZmNAC111* gene reportedly accumulated abundant messenger RNA against drought in maize plants (Zhang, Lei, et al., 2018). Various transcriptional factors, such as the *HD-ZIP* gene family, have also been shown to play a vital part in plant adaptation to water deficiency by regulating physio-biochemical processes (Sharif et al., 2021).

Recent reports have recommended that hydraulic signals, calcium waves, eclectic currents, mRNAs, ROS and phytohormones contribute to drought stress responses (Kudla et al., 2018). Furthermore, under critical drought stress, plants tend to accumulate branched-chain amino acids (e.g., valine, leucine and isoleucine) and other amino acids (e.g., threonine, lysine and methionine) (Pires et al., 2016). In addition, metabolic profiling of ABA synthesis mutant *nced3* showed that branched-chain amino acids and aminobutyric acid tend to accumulate in plants under drought stress (Urano et al., 2009). Latest reports also recommend that plant acetate accumulation activates the jasmonic acid pathway, increasing drought tolerance (Fàbregas & Fernie, 2019; Kim et al., 2017; Rasheed et al., 2018).

3 | ROLE OF NANOTECHNOLOGY IN AGRICULTURE: AN OVERVIEW

The natural surroundings of plants are uncovered to hostile environmental factors, including the rapidly increasing population, which threatens the agricultural industry (Farooq et al., 2022;

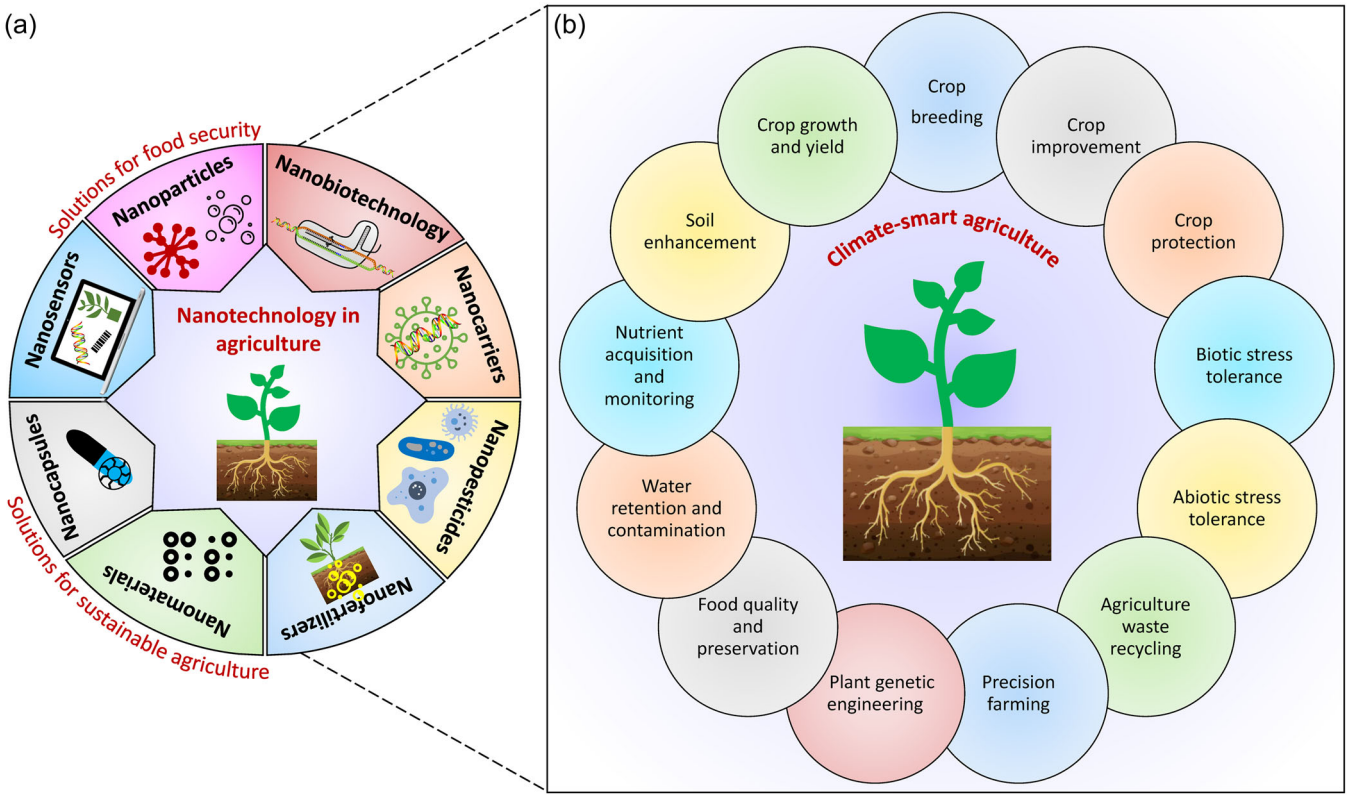


FIGURE 1 Dynamic role of nanotechnology in agriculture. (a) Some nanotechnological tools used in agricultural nanotechnology. (b) Application of nanotechnological tools to improve agricultural systems under stressed or controlled conditions.

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Sonmez et al., 2022). Current agricultural practices appear unsustainable due to the threat of climate change, deficiency of arable land, and the ever-rising cost of pesticides, water, fertilisers and agrochemicals. Precision farming can overcome these environmental constraints and amplify agricultural productivity to guarantee global food safety (Farooq et al., 2022; Jeger et al., 2021; Neme et al., 2021; Singh, Tiwari, et al., 2021). The recent use of nanotechnology (including NPs, nanobiotechnology, nanocarriers, nanofertilizers, nanopesticides, nanomaterials, nanocapsules and nanosensors) in agricultural systems has seen promising results (Figure 1); however, the materials used must be flexible to adjust to environmental changes based on plant needs and thus requires the design/development of precise nanomaterials for agriculture and food safety (Usman et al., 2020; Vithanage et al., 2023; Zahedi et al., 2019; Zulfiqar & Ashraf, 2021).

Nanoporous materials can be designed to deposit and distribute water slowly in agricultural zones facing severe water deficits (Niazian et al., 2021; Ranjan et al., 2022). Nanomaterials could also deliver the right amount and form of nutrients and pesticides with high precision based on plant needs, decreasing unnecessary chemical use and their environmental impact due to leached mineral residues (Hu & Xianyu, 2021; Usman et al., 2020). However, there are challenges involved in designing effective and nontoxic nano-enabled agrochemicals that are safer than their counterparts for plants and agroecosystems, providing eco-friendly solutions for modern agriculture (Abdollahdokht et al., 2022; Hu & Xianyu, 2021; Ranjan et al., 2022; Usman et al., 2020). Recent improvements in genetic engineering tools and engineered nanomaterials have facilitated the targeted distribution of nanocarriers (mRNA and sgRNA) for genetic crop alteration (Demirer et al., 2021; Yan et al., 2022).

While nanotechnology uses have received some negative responses related to environmental pollution, food safety and safe disposal (Jiang, Song, et al., 2021; Liu et al., 2021), requiring further investigation to persuade growers and the community of its benefits to food security and environmental safety, it remains a promising and innovative tool in agronomy that can contribute to achieving sustainable agriculture and addressing 21st-century challenges (Figure 1).

4 | NPs IMPROVE PLANT HEALTH AT DIVERSE DEVELOPMENTAL STAGES UNDER STRESS CONDITIONS

Plant responses to diverse abiotic stresses are affected mainly by stress severity, exposure duration and plant developmental stage (Ding & Yang, 2022; Rivero et al., 2022; Zandalinas et al., 2021). Adverse conditions can have distinctive effects on plant performance at different phenological stages, as can the exogenous application of plant modulators to mitigate stress-induced undesirable effects. The available literature suggests a developmental-dependent response of plants to various types of exogenous materials in terms of accelerating or delaying growth characteristics (Kupke et al., 2021; Ostrowska et al., 2021; Ranjan et al., 2022). Recent studies have evaluated the use of appropriate concentrations of NPs for alleviating the antagonistic effects of abiotic factors, for example, salinity and drought (Abdelsalam et al., 2023; Usman et al., 2020; Zahedi et al., 2019; Zulfiqar & Ashraf, 2021). Several types of NPs (e.g., Ag-NPs and ZnO-NPs) activate the antioxidant defence systems in different plant tissues, reducing ROS and improving growth (Acharya et al., 2020; Mahakham et al., 2017; Szőllősi et al., 2020; Waqas Mazhar et al., 2022). However, NP-mediated mitigation of various stresses highly depends on NP concentrations, plant species and plant developmental phase (Hu & Xianyu, 2021; Usman et al., 2020). The most common mechanisms underlying NP-induced effects on various developmental stages of stressed plants are shown in Figure 2.

Studies have shown that seed nano-priming enhances sprouting and seedling development more effectively than other priming methods using bulk and ionic materials (Abbasi Khalaki et al., 2021; do Espirito Santo Pereira et al., 2021; Kandhol, Singh, et al., 2022). Seed sprouting is an important and vulnerable developmental stage implying different metabolic adjustments that can overcome environmental stresses. NPs can break seed dormancy by increasing nutrient and water uptake, activating enzymes (such as CAT, SOD, amylases and proteases), and thus stimulating plant defence systems upon introduction to environmental stresses (Acharya et al., 2020; Mahakham et al., 2017; Szőllősi et al., 2020). This event likely improves seed vigour required for later seedling development. Metallic-NP seed priming has been used widely; for example, Ag-NP-primed aged rice (*Oryza sativa* L.) seeds had a superior propagation rate and seedling vigour compared to unprimed seeds and seeds treated with their ionic counterpart (Mahakham et al., 2017). The authors stated that upregulation of α-amylase activity and, thus, elevated soluble carbohydrate content facilitated rice seedling development. Nano-priming of rapeseed (*Brassica napus* L.) seeds with ZnO-NPs at 25, 50 and 100 ppm increased germination parameters under 150 mM NaCl stress due to enhanced proline and soluble sugar contents (El-Badri, Batool, Mohamed, et al., 2021).

Likewise, a recent study reported that Se-NPs and ZnO-NPs modulated ABA and gibberellin gene expression in germinating rapeseed under salinity stress, increasing the germination of primed seeds when compared with unprimed and hydro-primed seeds (El-Badri, Batool, Wang, et al., 2021). Rice seeds primed with ZnO-NPs (25 ppm) had higher growth performance and yield under drought stress than unprimed seeds (Waqas Mazhar et al., 2022). Increased osmoprotectant levels, including proline and ROS scavengers like SOD, CAT and peroxidase (POD), in the ZnO-NPs-primed plants were attributed to the higher drought stress tolerance (Waqas Mazhar et al., 2022). Similarly, TiO_2-NPs (60 ppm) priming of maize (*Zea mays* L.) seeds certainly influenced germination rate and seedling vigour under salinity stress, mediated by increased antioxidant enzyme activities (Shah et al., 2021).

Nanopriming can minimise impairment to the photosynthetic apparatus and ultrastructural alterations in plant cells under unfavourable situations by activating H_2O_2 signalling and the antioxidant defence system (Salam et al., 2022). Other nanomaterials,

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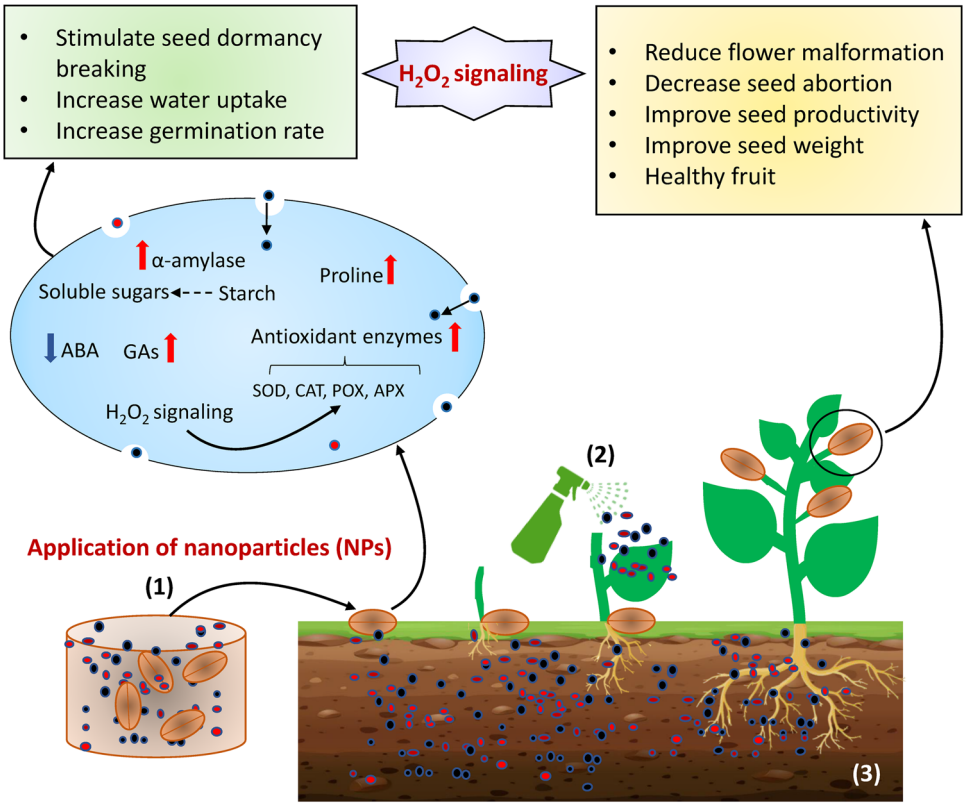


FIGURE 2 A putative schematic of the proposed mechanism underlying nanoparticle (NP) application to mitigate adverse signs of environmental stress at different plant developmental stages. Three common NP applications include (1) nano seed priming, (2) foliar spray and (3) soil mix with NPs/soil irrigation. For seed priming applications, NPs can be absorbed by the seed coat, facilitating water uptake and increasing the germination rate. NP exposure can also induce oxidative respiration, producing H_2O_2, which acts as a signalling molecule to stimulate seed germination-associated metabolic pathways, including increasing α-amylase activities and GA biosynthesis and decreasing abscisic acid biosynthesis. Moreover, the antioxidant defence system is activated via H_2O_2 signalling cascade. Foliar and soil NP applications can also improve plant growth by the same mechanism (i.e., H_2O_2 signalling), resulting in better seed productivity and healthier seeds. Red and blue arrows show positive and negative regulation, respectively.

such as carbon nanotubes, have improved plant stress tolerance. In a recent study, multi-walled carbon nanotubes at 90 ppm improved salinity tolerance in grape (*Vitis vinifera* L.) seeds, increasing the germination rate and seedling development, mainly by reducing malondialdehyde (MDA) content and lowering the tolerance capacity by activating the antioxidant enzymes system (Li et al., 2022). The positive effects of multi-walled carbon nanotubes on broccoli (*Brassica oleracea* L.) seedling growth under salt stress were attributed to higher aquaporin transduction, which increased water up-take and net CO_2 adjustment (Martínez-Ballesta et al., 2016). Based on the studies above, eco-friendly nanopriming methods increase water uptake via nanopores, boosting the antioxidant system, accelerating starch hydrolysis and thus improving the seed germination rate.

The application of NPs at the seedling stage can alleviate stress-induced growth reductions. The mechanism underlying the effect of NPs at this developmental stage is in line with seed germination. A pot experiment showed that the foliar treatment with ZnO-NPs on cucumber (*Cucumis sativus* L.) seedlings improved plant biomass under drought stress mainly by boosting both enzymatic and nonenzymatic antioxidative systems to decrease ROS generation and so MDA (Ghani et al., 2022). Similarly, applying ZnO-NPs notably enhanced plant growth-related traits, including fresh and dry weights, yield and photosynthetic pigments in salinity-stressed wheat at the vegetative and maturity stages (Adil et al., 2022). For other stresses, like antibiotics, TiO-NPs (50 ppm) added to soil improved nutritional quality, including iron, carbohydrate and protein contents, in wheat grain by 31%–42% (Amin et al., 2023). The application of functionalized NPs against biotic and abiotic stresses has gained attention. Several studies have investigated their role in various plant processes responding to different stressors. Graphene oxide-glycine betaine functionalized NPs at a suitable dosage (50 ppm) decreased the adverse effects of salinity stress in sweet basil (*Ocimum basilicum* L.) by improving photosynthetic components, membrane integrity and oxidant and non-oxidant metabolite accumulation (Ganjavi et al., 2021).

NPs can alter metabolic processes beyond the physiological and biochemical conditions of seed germination (Li, Liang, et al., 2021). Untargeted metabolomics analysis of watermelon (*Citrullus lanatus* L.) seedlings treated with Fe-NPs showed the upregulation of nonenzymatic antioxidants and triggered jasmonate-linked defence responses, indicating the potential of Fe-NPs for stimulating signalling pathways (Kasote et al., 2019). Furthermore, ZnO-NPs and single-walled carbon nanohorns

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increased salinity stress tolerance of *Sophora alopecuroides* seedlings by readjusting carbon/nitrogen metabolic pathways, glycolysis and the citric acid cycle to produce energy for plant growth (Wan et al., 2020). Various abiotic stresses affect reproductive development, a vital level in the life phase of flowering plants (Salehi, Rad, et al., 2021). Literature has demonstrated the susceptibility of key generative processes, such as phase transition, flowering induction, sporogenesis and gametogenesis, to environmental fluctuations, which can result in male sterility and seed abortion (Du, Zhao, Chen, Yao, Xie, 2020; Salehi, Chehregani, et al., 2021; Salehi, Rad, et al., 2021). There are few studies on the result of NPs on the reproductive stage of plant development under stress conditions. However, the timely use of NPs can improve yield components, including seed productivity and healthy fruit. For example, foliar treatment of SiO_2-NPs and TiO_2-NPs to barley significantly improved seed weight and yield under drought (Ghorbanian et al., 2017). Mango (*Mangifera indica* L.) trees in full bloom and 1 month after NaCl stress that received foliar treatment of ZnO-NPs and Si-NPs (50–150 ppm) responded positively in terms of growth, nutrient uptake, carbon assimilation, proline content and antioxidant enzyme activity, which markedly reduced flower malformation and seed abortion, improving annual fruit productivity (Elsheery et al., 2020). Soil treated with Fe-NPs upregulated photosynthesis and decreased oxidative stress in wheat plants (*Triticum aestivum* L.) under combined cadmium and drought stress, thus improving growth and grain productivity (Adrees et al., 2020). Another investigation directed that the incorporation of three micronutrient NPs (ZnO, B_2O_3 and CuO) through soil and foliar application 3 weeks after germination increased wheat growth and grain yield by 33%–36% under drought stress (Dimkpa et al., 2017). The study highlighted that NP soil application was more efficient as compared to foliar treatment (Dimkpa et al., 2017). Nonetheless, more investigations are required to evaluate the effect of NPs on the reproductive stage of plant development under stressful conditions.

To sum up, NP application, particularly nanopriming and foliar exposure, regulates the molecular machinery of seed germination, seedling expansion and plants maturity by upregulating the expression levels of oxidative stress-related genes, proteins and metabolites accumulation to strengthen defence system-mediated tolerance (Figure 2), thus enabling plants to tackle with various environmental factors by adjusting key signalling molecules, including H_2O_2 and responsible transcription factors. However, the mechanism underlying the interactions between NPs and plant reproductive stages has received little attention; further studies on various omics analyses are needed, along with phenotypical and agronomic facets of plant tolerance to various abiotic stresses.

5 | APPLICATION OF NPs TO IMPROVE PLANT STRESS TOLERANCE

Food safety is a matter of concern for the growing population due to inadequate reserves and ongoing climate change worldwide. Climate variation is causing several environmental factors that significantly influence plant growth and output (Farooq et al., 2022; Kumar et al., 2021; Rivero et al., 2022; Wang et al., 2021). Consequently, it is important to facilitate the improved adaptation of crop plants through hormone management, stimulation of enzymatic defence systems, expression of stress-responsive genes, evasion of water deficit trauma, and management of nutrient movement and apprehension (Cooper & Messina, 2023; Raza, Mubarik, et al., 2023; Rivero et al., 2022). Recent innovations in plant nanotechnology (e.g., NP application) can boost crop production in the current hostile environment, mainly subjected to drought and salinity stresses (Figure 3) (Jiang, Song, et al., 2021; Kandhol, Jain, et al., 2022; Usman et al., 2020; Zulfiqar & Ashraf, 2021). The findings below demonstrate that nanotechnology can improve the negative consequences of drought and salinity stress in different crop plants.

5.1 | Drought stress management by NPs

In an open environment, drought stress limits plant growth and production (Bhardwaj & Kapoor, 2021; Cooper & Messina, 2023; Raza, Mubarik, et al., 2023; Varshney et al., 2021; Yang & Qin, 2023). NPs have the ability to improve the adverse consequences of drought stress by inducing biochemical and physiological readjustments and modifying gene expression (Table 1). Different types of NPs have been established for balanced crop production, enhanced yield and reduced economic and nutritional failures under drought stress (Kandhol, Jain, et al., 2022).

For instance, foliar application of ZnO-NPs (50 and 100 ppm) in eggplant (*Solanum melongena* L.) 30 and 45 days after transplanting increased RWC and membrane stability index and increased leaf and stem anatomical arrangements and photosynthetic efficacy against drought stress (Semida et al., 2021). Soil amended with ZnO-NPs at different concentrations (1, 3 and 5 mg kg^{-1} Zn) alleviated drought effects in sorghum (*Sorghum bicolor* L.) and enhanced grain yield (22%–183%) and the gain of essential nutrients like potassium (16%–30%), nitrogen and zinc (94%) in grain (Dimkpa et al., 2019). Foliar spray of 0.1% and 0.05% ZnO-NPs on 14-day-old Moringa peregrine seedlings augmented drought tolerance by significantly decreasing Chl degradation and enhancing antioxidant activities and phenolic contents (Foroutan et al., 2019). A 1% chitosan NPs (CS-NPs) foliar treatment to 45-day-old cape periwinkle (*Catharanthus roseus*) seedlings mitigated drought effects by inducing gene expression of alkaloid biosynthesis, enhancing proline accumulation and antioxidant activities such as CAT and APX, and reducing MDA and H_2O_2 contents (Ali et al., 2021). Drought-stressed maize plants supplemented with Cu-NPs via seed priming had enhanced Chl, carotenoids and anthocyanin contents and reduced ROS, which increased grain yield (Van Nguyen et al., 2022). Priming wheat seeds with a colloidal solution of Cu-Zn-NPs decreased the negative impacts of drought stress by increasing antioxidative activities, RWC, leaf area and photosynthetic pigments and decreasing the buildup of thiobarbituric acid reactive elements (Taran et al., 2017).

Applying FeO-NPs in Murashige and Skoog medium alleviated drought stress by improving photosynthetic pigments, morphological growth, proline contents, carbohydrates and proteins with no toxic

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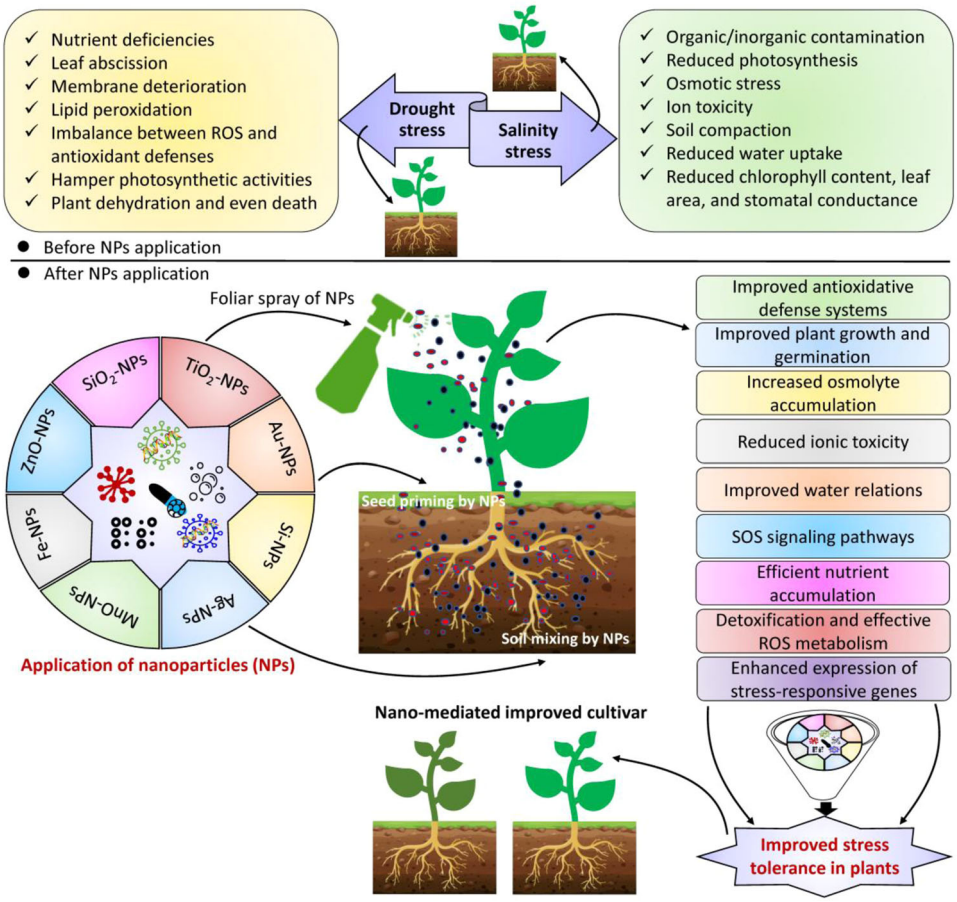


FIGURE 3 A model indicating how nanoparticle application (foliar spray, seed priming and soil mixing with nanoparticles [NPs]) can help improve plant health and tolerance to drought and salinity stress.

effects in strawberry (*Fragaria×ananassa* Duch.) plants (Havas & Ghaderi, 2018). Moreover, Fe-NP soil application (1 week before sowing) under cadmium and drought stress decreased oxidative damage and cadmium uptake and enhanced photosynthesis and iron concentrations in wheat grains (Adrees et al., 2020). Maize seed priming with 25 ppm carbon nanotubes (CNTs) improved the percentage and speed of seed germination, carotenoids, total Chl, and Chl a/b contents under drought stress (Shahriari et al., 2019). In soybean (*Glycine max* L.), supplementing seeds with single-walled CNTs improved plant germination, fresh seed weight, root and shoot lengths, POD and CAT activities, and MDA and H_2O_2 contents under severe water deficiency (Sun et al., 2020). Similarly, SiO_2-NPs increased drought tolerance by enlightening seed germination, antioxidative defence system, water uptake efficiency, amylase activity and seedling growth in wheat (Akhtar et al., 2021).

Under drought stress, soil application of Si-NPs significantly increased carotenoids, total Chl, and Chl a/b in barley (*Hordeum vulgare* L.), with enhanced carotenoid, Chl contents, shoot biomass and antioxidant enzyme activities during the post-drought recovery (Ghorbanpour et al., 2020). In field trials, foliar treatment with Si-NPs at the 10–12-leaf stage of sugar beet (*Beta vulgaris* L.) protected plants against drought by increasing growth, RWC, dry weight, total leaf area, Chl levels and soluble sugar content while decreasing leaf aging (Namjoyan et al., 2020). Supplementation of saffron crocus (*Crocus sativus* L.) corms with Ag-NPs ameliorated adverse drought effects by upregulating the beta-carotene hydroxylase gene and improving antioxidant activities and photosynthetic colourings (Sabertanha et al., 2017). Exogenous construction of Ag-NPs by *Tephrosia apollinea* plants ameliorated drought effects by increasing antioxidant activities and plant biomass and minimising oxidative injury and cell death (Ali et al., 2019).

Drought tolerance in barley improved with foliar sprays of nano-iron and manganese at different developmental stages, increasing yield and repairing the damage from water shortage (Zahedi & Alipour, 2018). Similarly, foliar spray of manganese nano-chelates to soybean at two stages (V4 and 1 week later) reduced drought effects by boosting Chl, leaf area, grain production, dry weight and nutrient uptake (Vaghar et al., 2021). Furthermore, foliar spray of manganese nano-chelates 1 week before and after irrigation increased carotenoid and Chl levels and reduced water stress in mung bean (*Vigna radiate* L.) (Sanavi & Mohammad, 2018). Under drought stress, potassium-NPs significantly improved proline, glycine, betaine, root and shoot dry weights, plant growth and physiological traits in pot marigolds (*Calendula officinalis*) (Erfani et al., 2021). Soil application of

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TABLE 1 Examples of nanoparticle applications to confer drought stress tolerance in different plant species.

Type of nanoparticles (NPs)	Plant species	Concentration	Application type	Protective impact of NPs on stress tolerance	References
Ag-NPs	*Crocus sativus* L.	55 and 110 ppm	Foliar	Mitigated adverse drought effects and improved catalase (CAT), peroxidase (POD), ascorbic acid peroxidase (APX), PAL, chlorophyll (Chl) b, carotenoids and phenylalanine	Sabertanha et al. (2018)
C-NPs	*Zea mays* L.	CNT; 25 and 50 ppm	Seed priming	Improved seed germination rate and percentage, total Chl, Chl a and b, carotenoids and drought tolerance	Shahriari et al. (2019)
K-NPs	*Zea mays* L.	0, 100 and 200 ppm	Foliar	Enhanced seed K and N and shoot Cu, Mn and Si concentrations and inhibited the adverse consequences of drought stress	Aqaei et al. (2020)
ZnO-NPs	*Zea mays* L.	100 ppm	Soil	Improved photosynthetic carbon assimilation, carbohydrate metabolism and antioxidant enzymes to prevent the disruption of mitochondria and chloroplasts	Sun et al. (2021)
Cu-NPs	*Triticum aestivum* L.	0, 3, 5 and 7 ppm	Foliar	Improved Chl stability index, leaf succulence, leaf content, stomatal conductance, nutrient uptake, water retention, yield and drought tolerance	Ahmed et al. (2021)
Fe_3O_4-NPs	*Setaria italica* L.	5, 10, 15, 20, 50, 90 and 120 ppm	Soil	Enhanced Chl, soluble sugars, proline content, plant growth and drought tolerance without any toxic effects	Sreelakshmi et al. (2021)
ZnO-NPs	*Solanum melongena* L.	0, 50 and 100 ppm	Foliar	Enhanced growth, physiology, photosynthetic rate, fruit yield and water productivity	Semida et al. (2021)
SiO_2-NPs	*Triticum aestivum* L.	150 ppm	Soil	Enhanced seedling growth, yield and drought tolerance and upregulated antioxidant enzyme activities	Akhtar et al. (2021)
Mn-NPs	*Glycine max* L.	Nano-chelates of manganese with iron and zinc	Foliar	Improved micronutrient contents and seed yield	Vaghar et al. (2021)
CaO-NPs	*Onobrychis viciifolia* L.	0.5 and 1.5 ppm	Foliar	Improved plant growth rate, leaf development, H_2O_2, malondialdehyde (MDA), Chl content and gene expression	Ertuş and Yazıcılar (2023)
Se-NPs	*Triticum aestivum* L.	10 ppm	Foliar	Increased photosynthetic rate, photosynthetic pigments, gas exchange and enhanced drought tolerance by improving CAT, APX, and superoxide dismutase (SOD) activities	Omar et al. (2023)
ZnO-NPs	*Triticum aestivum* L.	50, 100 and 150 ppm	Foliar	Improved total Chl, Chl a and b, and antioxidant defence systems and guarded crop from oxidative injury	Kausar, Hussain, et al. (2023)
TiO_2-NPs	*Solanum lycopersicum*	100 ppm	Foliar	Increased relative water content (RWC) and decreased proline and MDA contents	Cevik (2023)
CH-NPs	*Solanum lycopersicum* L.	60 and 90 ppm	Soil	Enhanced plant growth, yield and drought tolerance by gene expression modulation	Mohamed and Abdel-Hakeem (2023)

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TABLE 1 (Continued)

Type of nanoparticles (NPs)	Plant species	Concentration	Application type	Protective impact of NPs on stress tolerance	References
B_2O_3-NPs	*Pisum sativum* L.	12.5, 25 and 50 ppm	Foliar	Improved phenol accumulation, FRAP, DPPH and ABTS antioxidant capacities, and APX, SOD, GPX and CAT activities	Sutulienė et al. (2023)
ZnO-NPs	*Coriandrum sativum* L.	100 ppm	Foliar	Improved net photosynthetic rate, stomatal conductance, Chl b contents, total soluble sugars, total phenolic content and total flavonoid contents	Ahmed et al. (2022)
F_2O_3-NPs	*Vitis vinifera* L.	0.7 ppm	Foliar	Decreased MDA and H_2O_2 generation and enhanced CAT, GPX, GR, MDHAR and DHAR activities	Bidabadi et al. (2023)
Si-NPs	*Triticum aestivum* L.	30, 60, 90 and 120 ppm	Foliar	Decreased H_2O_2 and MDA contents and increased RWC, antioxidant enzyme activities (APOX, CAT and SOD), Chl and proline contents	Boora et al. (2023)
ZnO-NPs and SiO_2.NPs	*Solanum tuberosum* L.	0, 50 and 100 ppm and 0, 25 and 50 ppm	Foliar	Increased leaf gas exchange, photosynthetic pigments and leaf green index	Al-Selwey et al. (2023)
Mn_3O_4-NPs	*Zea mays* L.	500 ppm	Soil-root	Increased root length, fresh weight and total protein content and reduced H_2O_2 and MDA contents	Sun et al. (2023)
MS-NPs	*Arabidopsis thaliana* L.	0–5,000 ppm	Foliar	Improved root length, lateral root count, leaf surface and shoot biomass	Tran et al. (2023)
ZnO-NPs	*Dracocephalum kotschyi* L.	10 and 20 ppm	Foliar	Enhanced Chl, sugar, proline contents and antioxidant enzyme activities (SOD, GPO and to some extent PPO)	Karimian and Samiei (2023)
ZnO-NPs and SiO_2-NPs	*Solanum tuberosum* L.	0, 50 and 100 ppm and 0, 25 and 50 ppm	Foliar	Improved tuber dry weight, specific gravity, ascorbic acid, starch and total soluble solids	Seleiman et al. (2023)
Zn-NPs	*Brassica rapa* L.	100, 500 and 1000 ppm	Foliar	Increased plant height, biomass, root/turnip length, turnip diameter, antioxidant defence system, secondary metabolites and leaf photosynthetic pigments	Li et al. (2023)

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TABLE 2 Examples of nanoparticle applications to confer salinity stress tolerance in different plant species.

Type of nanoparticles (NPs)	Plant species	Concentration	Application type	Protective impact of NPs on stress tolerance	References
Fe_2O_3-NPs	*Dracocephalum moldavica* L.	60 ppm	Foliar	Improved total leaf area and nonenzymatic and enzymatic antioxidants	Moradbeygi et al. (2020)
C-NPs	*Lactuca sativa* L.	3000 ppm	Seed priming	Promoted lateral root growth, seed germination and Chl content in seedlings	Baz et al. (2020)
Ag-NPs	*Spinacia oleracea* L.	10, 20, 40, 80 and 100 ppm	Foliar	Improved seed germination and salinity tolerance	Ali Naghi Zadeh et al. (2020)
Mn_3O_4-NPs	*Cucumissativus* L.	1 and 5 ppm plant^{-1}	Foliar	Alleviated oxidative stress, maintained biomass and increased antioxidant defence system, photosynthesis and metabolome of shikimate and phenylpropanoids pathways	Lu et al. (2020)
K-NPs	*Pisum sativum* L.	50 and 100 ppm (nano K with N and P)	Foliar	Enhanced plant growth, yield, mitotic index and salinity tolerance and decreased chromosomal aberrations	El-Hefnawy and Nano (2020)
SiO_2-NPs	Gerbera	0, 25 and 50 ppm	Foliar	Improved antioxidant enzymes, photosynthesis, ROS capture, osmotic balance of cells and Ca^{2+} (25.3%) and K^+ (27.1%) uptake and decreased Na^+ (6.3%) absorption	Hajizadeh et al. (2021)
Ag-NPs	*Satureja hortensis* L.	0, 40, 60 and 80 ppm	Seed priming	Enhanced germination average, seedling growth, shoot length and plant tolerance to salinity stress	Nejatzadeh (2021)
ZnO-NPs	*Lycopersicon esculentum* Mill.	10, 50 and 100 ppm	Foliar	Enhanced shoot and root lengths, total proteins, Chl, photosynthetic attributes, plant growth, antioxidant enzyme activities (catalase [CAT], superoxide dismutase [SOD], and POX) and improved salinity tolerance	Faizan et al. (2021)
ZnO-NPs	*Carthamus tinctorius* L.	17 ppm	Foliar	Improved salt tolerance, antioxidant enzyme activities, and osmolyte content and decreased proline and malondialdehyde (MDA) contents	Yasmin et al. (2021)
Cu-NPs	*Zea mays* L.	100 ppm	Soil	Improved antioxidant activities, shoot and root lengths, and dry and fresh weights and decreased oxidative damage and lipid peroxidation	Noman et al. (2021)
Se-NPs	*Chenopodium quinoa* L.	1 ppm	Seed priming	Increased photosynthetic pigments, compatible solutes, reduced oxidative injury and sodium uptake and protected cell membranes	Ashraf Ganjouii et al. (2023)
ZnO-NPs	*Oryza sativa* L.	50 ppm	Foliar	Increased root length, root fresh weight, root dry weight, root K^+ content and root antioxidant enzymatic activities	Singh et al. (2023)
TiO_2-NPs	*Triticum aestivum* L.	25, 50, 75 and 100 ppm	Foliar	Improved germination traits and physio-morphic parameters (plant length, plant fresh and dry weights, leaf number, leaf area, relative water content [RWC], MSI and Chl contents)	Badshah et al. (2023)
CTS-HPMC-Mel NPs	*Mentha spicata* L.	1000 ppm	Seed priming	Enhanced morphological traits, proline, antioxidant enzymatic activities, and the dominant constituents of essential oil profile	Gohari, Farhadi, et al. (2023)
CS-NPs	*Oryza sativa* L.	50 ppm	Seed priming	Improved germination, seedling vigour and biochemical and antioxidant responses	Soni et al. (2023)

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TABLE 2 (Continued)

Type of nanoparticles (NPs)	Plant species	Concentration	Application type	Protective impact of NPs on stress tolerance	References
GO-Pro NPs	*VITIS VINIFERA* L.	50 and 100 ppm	Foliar	Enhanced antioxidant enzyme activities, proline and leaf RWC and reduced EL, H_2O_2, and MDA contents	Zahedi et al. (2023)
CMgO-NPs	*Oryza sativa* L.	100 ppm	Seed priming	Enhanced root length, dry biomass, plant height and tetrapyrrole biosynthesis and induced antioxidative enzyme activities (CAT, POD and SOD)	Song et al. (2023)
OA-POSS-NPs	*Ocimum basilicum* L.	25, 50 and 100 ppm	Foliar	Improved photosynthetic pigment content, adjusted Chl fluorescence, and triggered nonenzymatic (phenolic content) and enzymatic antioxidant components	Gohari, Panahirad, et al. (2023)
ZnO-NPs	*Triticum aestivum* L.	0, 20,000, 40,000 and 60,000 ppm	Applied coating	Increased film hardness, decreased moisture absorption and increased contact angle	Gohari, Modiri, et al. (2023)
Si-NPs	*Zea mays* L.	75 ppm	Soil	Improved plant growth by increasing nutrient accessibility (P and K) and physiological traits, and lowering cationic ratios	Rizwan et al. (2023)

potassium-NPs to maize boosted nutrient uptake, seed potassium and nitrogen concentrations and shoot copper, manganese, and silicon contents, inhibited the adverse possessions of drought stress, and advanced drought tolerance (Aqaei et al., 2020).

Moreover, soil application of TiO_2-NPs stimulated drought tolerance in wheat by improving fresh and dry weights, root and shoot lengths, osmolyte content, membrane stability and total Chl (Mustafa et al., 2021). Under water deficit, TiO_2-NP application (at the 4–6 leaf stage and 2 weeks later) improved drought tolerance and maize grain yield by enhancing leaf antioxidant activities (SOD, APX and CAT) and increasing leaf proline content (Karvar et al., 2022). Likewise, exogenous treatment with nitric oxide improved the defensive influences of TiO_2-NPs on plant growth, photosynthetic performance, and the antioxidative system of wheat seedlings under water deficit stress (Faraji & Sepehri, 2020). Metal oxide-NPs ameliorated drought-induced ROS via osmolyte aggregation, improving crop water balance and osmotic adaptation (Alabdallah et al., 2021). In wheat at the trifoliate stage, 30 ppm Se-NPs alleviated drought stress and enhanced shoot length, shoot fresh and dry weights, plant height, root length, root fresh and dry weights, leaf area, leaf number and leaf length (Ikram et al., 2020).

Priming with Fe_3O_2-NPs enhanced wheat germination, Chl a and b, carotenoids and proline contents and antioxidant (SOD, POD and APX) enzyme activities under drought stress (Noor et al., 2022). Rice seed priming with ZnO-NPs alleviated drought stress and improved plant height, total Chl contents, and plant fresh and dry weights; the ZnO-NPs also enhanced proline levels and improved SOD, CAT and POD activities by 11%, 13% and 38%, correspondingly, facilitating plants to combat water shortage stress (Waqas Mazhar et al., 2022). Foliar ZnO-NPs application to cucumber seedlings under drought stress increased proline, glycine betaine, free amino acids and sugar contents and decreased lipid peroxidation and ROS levels (Ghani et al., 2022).

5.2 | Salinity stress management by NPs

Salinity significantly reduces plant growth and production (Giordano et al., 2021; Melino & Tester, 2023; Raza et al., 2022). Under salinity stress, NP application can help mitigate the adverse impacts by increasing osmolyte production, antioxidant activities and stress-related gene expression (Table 2). Nanoparticle application can also improve growth-related traits and total yield under salinity stress.

Foliar application of CS-NPs at 15-day intervals from 2 weeks after transplanting mitigated deleterious salinity effects in *Catharanthus roseus* by inducing the antioxidative defence system to help scavenge ROS and activate the transcript levels of ORCA3, GS and MAPK3 genes, increasing alkaloid buildup and improving protection under salt stress (Hassan et al., 2021). Application of TiO_2-NPs, combined with quarter-strength Hoagland solution, to Moldavian dragonhead (*Dracocephalum moldavica* L.) at the 12-leaf stage under saline conditions increased plant growth, antioxidant enzyme activities and essential oil contents,

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improving agronomic traits and decreasing H_2O_2 levels (Gohari et al., 2020). Likewise, priming with 0.01 ppm S-NPs improved antioxidant status, photosynthetic pigments, ionic relations and nitrogen metabolism in wheat under salinity stress (Saad-Allah and Ragab 2020). Foliar spray of nano-zinc oxide (100 ppm) and nano-silicon (150 ppm) to mango improved plant growth, carbon assimilation, nutrient uptake, antioxidant enzyme activities and annual fruit yield, and significantly decreased flower malformation under salt stress (Elsheery et al., 2020). Under salt stress, cotton (*Gossypium hirsutism* L.) seed priming with antioxidant poly(acrylic acid)-coated cerium oxide-NPs significantly improved root length, roots dry and fresh weight and root vitality, altered root anatomical organisation and reduced ROS production (An et al., 2020). Leaf spraying of CeO_2-NPs (four times, 24 h apart) improved the antioxidant enzyme activities and growth parameters in *Dracocephalum moldavica* L. under salinity stress (Mohammadi et al., 2021).

Foliar spray of SiO_2-NPs improved Chl content, regulated sodium levels, induced potassium uptake and declined cell wall impairment in banana cultivar 'Grand Nain' under salt and water deficit (Mahmoud et al., 2020). Similarly, seed priming lettuce with 0.3% soluble carbon-NPs significantly improved seed sprouting, lateral root development and Chl content under salt conditions (Baz et al., 2020). In *Eucalyptus tereticornis*, soil application of FeO-NPs alleviated salinity stress by upregulating *NHX1*, *SOS1* and *HKT1* to increase shoot length, Chl content, and CAT and POD activities (Singh, Sillu, et al., 2021). Soil irrigation of Si-NPs boosted cucumber productivity under salt and water deficit conditions by improving nutrient uptake (Alsaeedi et al., 2019). In flaxseed/linseed (*Linum usitatissimum* L.), foliar spray of Ag-NPs minimised the effect of salinity stress by significantly improving photosynthetic pigments and soluble protein, proline and soluble carbohydrate contents (Khalofah et al., 2021). Ag-NPs also decreased H_2O_2 and MDA contents and improved enzymatic and nonenzymatic antioxidant activities. Ag-NPs may help boost linseed crop productivity in salt-stressed environments (Khalofah et al., 2021).

Foliar treatment with salicylic acid and nano-Fe_2O_3 NPs at the seven-leaf and flowering stages of ajowan plants relieved salinity toxicity and enhanced plant growth by promoting H^+-ATPase and H^+-PPase activities and avoiding nutrient inequality (Ghassemi-Golezani & Abdoli, 2021). Furthermore, foliar spray of Fe_3O_4-NPs at tillering and flowering stages lightened the contrary results of salinity stress on wheat by enlightening growth, Chl content, soluble proteins, glutathione, SOD, and antioxidant defence systems and decreasing MDA levels (El-Saber et al., 2021). Under salinity stress, foliar spray of ZnO-NPs to 25-day-old tomato seedlings boosted Chl content, root and shoot lengths, leaf area, biomass, protein content and antioxidative activities (e.g., SOD, POX and CAT) in tomato (Faizan et al., 2021).

Irrigating 30-day-old broad bean (*Vicia faba* L.) seedlings with calcium phosphate NPs (CaP-NPs) increased plant yield, antioxidants activities, and soluble sugars, proline and total phenolic contents under salt stress (Nasrallah et al., 2022). Foliar spray of ZnO-NPs to rapeseed at the rosette stage mitigated the negative effects of salt stress by enhancing the Hill reaction, avoiding root ion leakage, and upregulating the expression pattern of *ARP* genes (Hezaveh et al., 2019). Moreover, foliar treatment with Zn-NPs to 3-week-old cotton plants improved growth by enhancing leaf, stem and boll growth under saline conditions (Hussein and Abou-Baker 2018). In tomatoes, a soil mixture containing Cu-NPs minimised the opposing possessions of salinity stress by increasing antioxidative enzyme activities, activating nonenzymatic and enzymatic defence systems, enhancing the potassium and sodium ion ratio, and upregulating *SOD* gene expression and jasmonic acid pathways (Hernández-Hernández et al., 2018).

Under salt stress, 2-year-old grapevine cuttings with eight leaves treated with carbon-NPs quantum dots improved antioxidant activities, leaf fresh and dry weights, and Chl, photosynthetic pigments, proline and phenolic contents in grapevine (Gohari, Panahirad, et al., 2021). The Au-Ag alloy NPs improved salt tolerance by improving GPX and CAT activities and soluble sugar contents in *Mentha piperita* (Aliakbarpour et al., 2020). Priming with Mn-NPs ameliorated the toxic consequences of salinity stress by increasing root growth and *MnSOD* expression in chilli (*Capsicum annuum* L.) (Ye et al., 2020). K_2SO_4-NPs in Hoagland solution relieved the negative influences of salinity by increasing antioxidants, CAT activities and proline content, decreasing electrolyte leakage and enhancing the physiological response of alfalfa (El-Sharkawy et al., 2017). Under saline conditions, SiO_2-NP application (500 ppm) three times per week reduced salt damage by improving Chl content and plant growth (Mahmoud et al., 2022). Seed priming with CeO_2-NPs boosted seed sprouting, root length, shoot length, dry seedling weight and ROS-scavenging capabilities and upregulated the expression of salicylic acid biosynthesis-associated genes in rapeseed under salinity stress (Khan et al., 2022). Under salt stress, BioSe-NPs in culture media upgraded the phenotypic features of rapeseed seedlings by triggering antioxidant enzymes involved in ROS decontamination, modulating enzyme-associated gene expression patterns, decreasing ROS and MDA levels and increasing lateral root development by boosting *LBD16* gene expression (El-Badri et al., 2022).

In conclusion, the literature assessed in the above sections (improving drought and salinity stress) has emphasised the potential aids of several types of NPs for agricultural applications. However, it is important to evaluate the risks and constraints associated with NPs/nanomaterials in agricultural use, including their environmental influence, economic sustainability and functional performance. For instance, the concerns raised in the medical field, especially regarding carbon nanotubes (Hansen & Lennquist, 2020), cannot be overlooked. The use of carbon nanotubes in agriculture increases several concerns, and the primary concern is their impending impact on human health and the environment (Rezaei Cherati et al., 2022). Thus, other NPs/nanomaterials should be examined before applying them to agricultural fields. Future considerations should focus on choosing the right NPs/nanomaterials based on specific agricultural relevance, such as types, size, concentration, targeted delivery and seed coating

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or priming for drought and salinity stress management. Moreover, it is also obligatory to perform extensive research and advancement to link the gap between laboratory experiments and field applications, adjusting NPs for practical use in the agriculture sector, mainly for developing stress-smart plants. Conditions such as long-term environmental sustainability, cost-efficiency and practical usableness should be carefully explored. By carefully exploring the risk assessment protocols and impending benefits with the allied hazards and constraints, we can deliver new ways to expand safe, applicable and sustainable NPs/nanomaterials to enhance agricultural production under stressful environments.

6 | NANO-MEDIATED GENOME EDITING FOR CROP IMPROVEMENT: A RAPIDLY EMERGING ERA

Conventional plant breeding is a labour-exhaustive and laborious method that requires significant effort to diversify the gene pool and crop improvement. In this context, crop productivity can be enhanced using NP-mediated genetic engineering techniques, introducing desirable genetic traits into crops to make them resistant to changing climate (Figure 4) (Cunningham et al., 2018). Genome editing is critical for improving crop invention, quality traits and increasing crop resistance to biotic and abiotic stresses such as drought and salinity (Chennakesavulu et al., 2021; Joshi et al., 2020; Nazir et al., 2022; Tariq et al., 2023; Yaqoob et al., 2023; Zaman et al., 2023). Genome editing methods, including zinc-finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeats (CRISPR) are revolutionary editing tools due to their high specificity and efficiency. Among these genome editing technologies, the CRISPR/Cas method has shown more encouraging results than ZFNs and TALENs because of its effortlessness and multiplexing range (Kausch et al., 2019; Saeed et al., 2020). TALENs and ZFNs are more complex and costly, with high off-target scores. Moreover, CRISPR/Cas is an easy and economical method that opens new horizons for crop expansion (Gao et al., 2020; Mahfouz et al., 2014; Yaqoob et al., 2023). The CRISPR/Cas technique also helps accelerate plant breeding and construct mutant plant libraries (Chen et al., 2019). To make use of genome editing tools, efficient transformation and rejuvenation procedures are essential for targeted manipulation of desired traits. While *Agrobacterium tumefaciens*-mediated transformation is widely used, it can be challenging and time exhausting, making it necessary to explore new techniques.

Using CRISPR technologies in plant genome editing requires an effective delivery method for substances (like DNA and RNA) into plant cells. This is typically achieved using plasmids or RNA protein

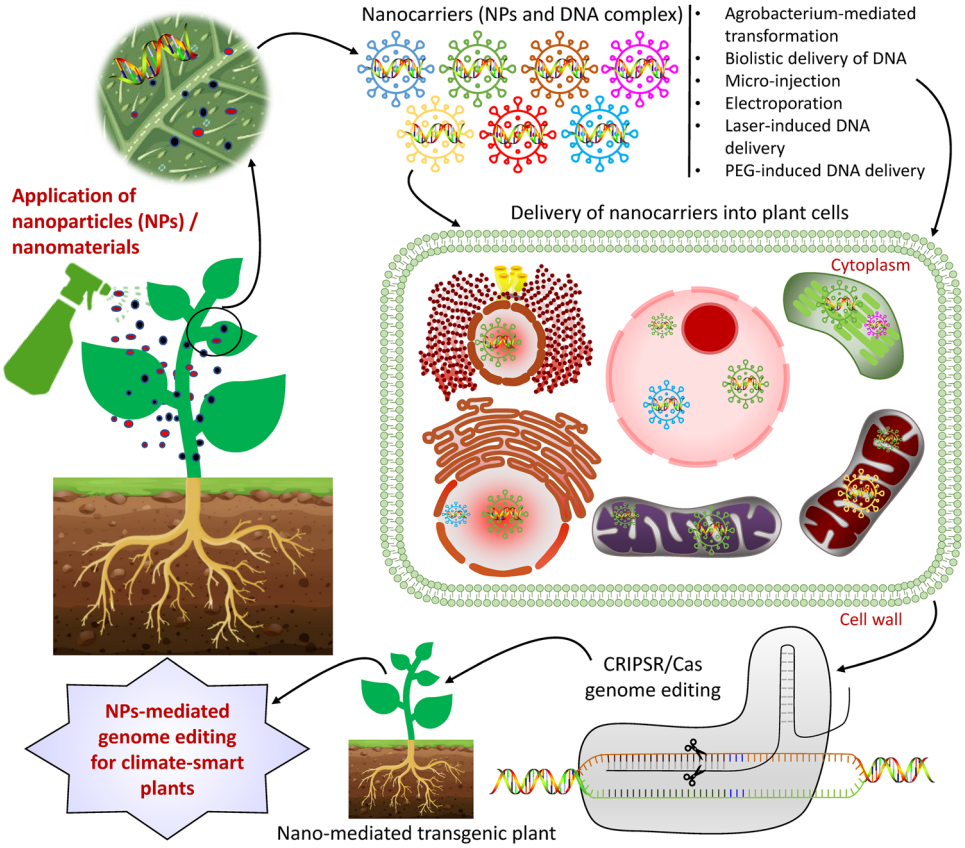


FIGURE 4 Proposed model of plant nanotechnology applications in nanoparticles (NPs)-mediated genome editing for improved crop breeding and climate-smart agriculture.

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complexes through gene gun *Agrobacterium*, cationic delivery, or viral infection (Sharma & Lew, 2022). However, using ribonucleoprotein complexes have lower off-target activity than plasmid-based delivery reagents into plant cells (Liu et al., 2017). Furthermore, recent advances in nanotechnology can assist deliver genetic supplies to plants for gene editing (Hofmann et al., 2020).

Nanotechnology has become a hopeful tool in plant genetic engineering for delivering genetic materials, such as RNA, DNA, or their complex with NPs, using different nanomaterials (Mujtaba et al., 2021). For example, CRISPR reagents like sgRNA could be delivered into the plant genome with carbon nanocarriers for effective gene knockdown (Demirer et al., 2020). The Cas-9 nanosystem carrier is suitable for targeting tissues and cells and lipid NPs (LNPs) can transport Cas9/sgRNA complexes and Cas9 ribonucleoprotein to tissues for genome editing (Cheng et al., 2020). The LNP delivery system of Cas9 is highly stable, with high editing efficiency and no off-target mutations (Qiu et al., 2021). Other methods for delivering genome editing reagents into targeted tissues use NPs poly (lactic-co-glycolic acid) that encapsulate CRISPR/Cas9 plasmids (Jo et al., 2020). Notably, NPs are involved in gene knockout using Cas9 and gene knock-in into the genome (Chou et al., 2020). As most of these experiments have been undertaken in animal or mammalian cells, there is a need to explore their potential in plant cells.

Nanobiotechnology techniques, especially NPs, have increased the accuracy of plant breeding by producing new gene combinations and reducing the time needed to eliminate unwanted genes from large populations (Pérez-de-Luque 2017). Magnetofection of bio-conjugated transgene–NP complexes have been described in dicots (Zhang et al., 2019), and NPs as delivery carriers are promising because they can transport NPs into plant cells without damaging tissues (Santana et al., 2020).

Speed breeding has emerged as a promising method for creating more cultivars quickly, mainly under normal conditions (Watson et al., 2018). Hence, combining genome editing, speed breeding and NPs can accelerate the breeding cycle and improve crop production (Figure 5) (Ahmar et al., 2021). Chimerically edited plants can be generated by delivering genome editing reagents and then subjected to speed breeding methods to develop many generations in a short time under controlled conditions for regeneration as transgene-free plants (Ahmar et al., 2021). A recent report demonstrated that CRISPR plasmids coated with carbon dots on the surface could be carried into plant cells through the foliar spray, leading to the successful editing of target genes (Doyle et al., 2019). Future studies should investigate editing stress-inducible genes via NP-mediated genome editing to boost crop productivity under stress conditions.

Other studies have investigated how a nano-biomolecule bioconjugated complex can be distributed force-impartially (Busch et al., 2019; Hu et al., 2020; Sapsford et al., 2013) without damaging altered cells or having opposing consequences on plants or the environment (Hu et al., 2020). These nanocarriers can deliver payloads to organelles with minimal residual impact on daughter cells (Hu et al., 2020). Therefore, combining plant nanotechnology with speed breeding and genome editing offers a promising approach to rapidly producing stress-smart plants to feed the growing population.

Optimising and developing integrated mechanisms are essential for serving humanity, such as the delivery of genome editing DNA and NPs. Future considerations include:

1. Assessing the safety of off-targets in CRISPR-edited crops with different NPs and the future implications of genome-edited plants.
2. Improving genome editing efficiency using multiplex genome engineering and designing guided RNA to minimise off-target activity.
3. Evaluating potential toxic impacts of diverse types of NPs as a delivery system for genome editing reagents on the plant genome.
4. Decreasing the overall size of cargo material for stable transformation while maintaining high editing efficiency.
5. Minimising direct contact of NPs with plant cells to avoid damaging the plant and interrupting important enzymatic functions that may lead to plant death.
6. Considering potential ROS generation under stress that could damage plant genetic material.
7. Developing more efficient and improved delivery methods of NPs that do not damage plant cells.

7 | CONCLUDING REMARKS AND FUTURE OUTLOOKS

In the aspect of global challenges modelled by climate change, the agricultural industry faces unprecedented challenges (e.g., drought and salinity stress) that affect global food production and supply. Emerging literature suggests that nanotechnology, particularly the use of NPs, can positively impact plant growth and ameliorate the harmful influence of drought and salinity. NPs have positively affected plant growth at physio-morphological, biochemical, and molecular levels, increasing drought and salinity stress tolerance. Still, it is urgent to consider not only the NP concentration, size properties and application method but also their composition, shape and surface chemistry. Recent investigations have emphasised the significant impact of NP composition, shape and surface chemistry on their effectiveness in increasing stress tolerance in plants (Avellan et al., 2019; Peng et al., 2020; Spielman-Sun et al., 2017; Zhang et al., 2022). Moreover, the size and shape of NPs can be manipulated to facilitate DNA delivery to plant cells (Zhang et al., 2022). Hence, a thorough understanding of the complete NP properties, including their composition, size, shape, surface chemistry and targeted application methods, is required to increase their competence in improving plant stress tolerance.

The use of NPs in the farming division has the potential to uphold sustainable agriculture by modifying the harmful outcomes of drought and salinity stress. However, further studies are essential

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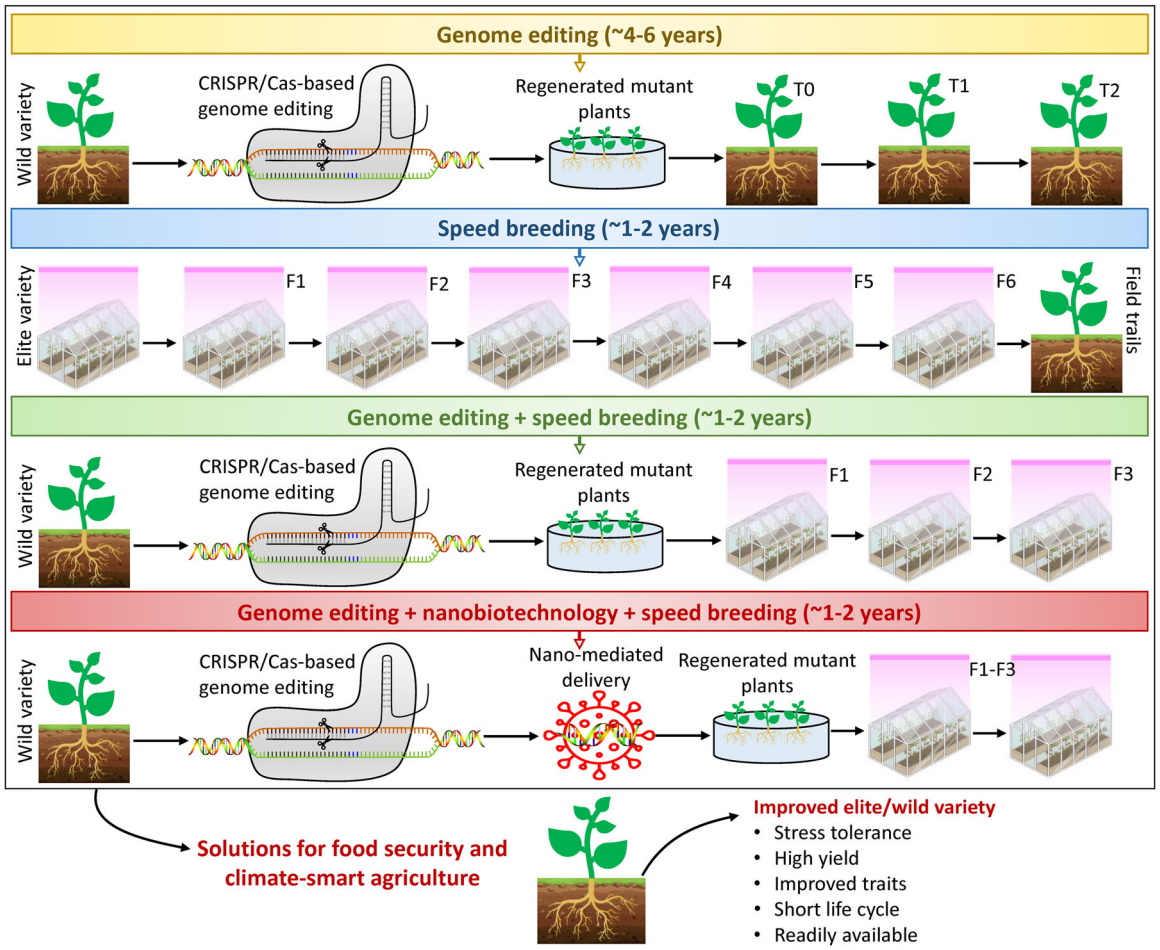


FIGURE 5 Schematic illustration showing the differences between genome editing (CRISPR/Cas system), speed breeding and nanobiotechnology presentations for crop improvement under controlled or stressed conditions. For detailed information on these tools and their applications for crop development, interested readers can refer to insightful reviews on (i) CRISPR/Cas-based genome editing to develop GMO-free characterised plants (Chen et al., 2019; Gao, 2021; Mahfouz et al., 2014; Tariq et al., 2023; Yin et al., 2017; Zhu et al., 2020), (ii) speed breeding to grow several generations in 1–2 years (Bhatta et al., 2021; Hickey et al., 2019; Samantara et al., 2022; Saxena et al., 2019; Watson et al., 2018) and (iii) nanotechnology-mediated genome editing to develop transgenic climate-smart plants (Ahmar et al., 2021; Cheng et al., 2020; Cunningham et al., 2018; Demirer et al., 2021; Mujtaba et al., 2021). Modified from Raza, Mubarik, et al. (2023).

to fully recognise the role of NPs under combined drought and salinity stress and to determine the best pathway for NP foliar uptake and mobility in plant leaves. Limited knowledge exists on the process of NP uptake and movement in plants. Therefore, there is a need to conduct more research on the translocation, accumulation and culture of nano-toxic-free plants to optimise their use in agriculture.

It is crucial to recognise NP behaviour in the leaf plant–soil continuum and how NPs upregulate host defence systems using proteomic, genomic and metabolomic approaches to validate the role of NPs in agricultural systems. However, the use of NPs also poses environmental contamination and human health challenges. If NPs bioaccumulate in edible plant tissues, they can adversely impact humans and livestock, which must not be overlooked. Consequently, it is essential to have fundamental know-how related to the relations of NPs and plants, environmental risks and the development of eco-friendly NPs before their mass application in agricultural practices. The biogenic development of NPs should be investigated, as these NPs are nontoxic due to their biodegradable characteristics. Extensive field assessments are needed to estimate the long-term application of NPs for ameliorating drought and salinity stress and promoting plant growth. Moreover, understanding the role of NPs at subcellular and molecular levels can help determine whether they act as stress inhibitors and stress indicators.

The use of NPs in agriculture has numerous benefits, including reducing environmental impurities, quick identification of stress, simple preparation, low toxicity and cost-effectiveness. Nanofertilizers, for example, have been developed using nanotechnology to enhance the nutrient uptake effectiveness of stressed plants. Properly treated, the use of NPs in agricultural sectors is generally safe for individuals and the environment.

Despite significant progress in crop genetics and breeding through nanotechnology, the transfer of exogenous DNA for genome editing by the CRISPR/Cas system remains challenging. Novel molecular nanocarriers, such as polymeric nanostructures and

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nanogels, could be used to improve the delivery of biomolecules for targeted genome editing in crop plants. While NP-mediated CRISPR/Cas9 complex supply is more advanced than other delivery approaches in plant science disciplines, additional research is required to confirm that the CRISPR system is effective, consistent and timely. Combining the CRISPR/Cas9 system with NPs could significantly innovate crop breeding and genetics.

Furthermore, combining genome editing (CRISPR/Cas9 system), nanobiotechnology (NPs) and speed breeding (short life cycle) could help to address the task of nourishing a growing global population while coping with the increasing threat of abiotic stress factors. This approach could accelerate crop breeding practices and lead to new crop varieties with augmented stress tolerance and advanced yields. This combination could also facilitate the creation of transgene-free crops, a key aspect of sustainable agriculture. However, further investigation is required to understand the mechanisms involved and address the potential risks associated with using NPs and genome editing in agriculture.

AUTHOR CONTRIBUTIONS

Ali Raza and Rajeev K. Varshney conceived the idea. Ali Raza, Sidra Charagh, Hajar Salehi, Saghir Abbas and Faisal Saeed contributed to the writing and literature search. Ali Raza, Kadambot H. M. Siddique, Gérrard Eddy Jai Poinern and Rajeev K. Varshney reviewed and edited the manuscript. All authors have read and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

ETHICS STATEMENT

This is a review article and ethics statement is not applicable to this study.

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