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REVIEW

Role of metal nanoparticles in organogenesis, secondary metabolite production and genetic transformation of plants under in vitro condition: a comprehensive review

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Abstract

Nanomaterials usually have specific characteristics due to their incredibly tiny size, which also increases their surface area, providing a more interactive surface. Compared to their macro-sized counterparts, these tiny nanoparticles exhibit a multitude of size-dependent properties. Plant tissue culture (PTC) plays an important role in bioactive chemical synthesis, mass cultivation, protection, genetic control, and plant enhancement. Different nanoparticles (NPs) are utilized to improve the tissue culture responses of explants. Various nanoparticles, including cobalt, copper, silver, gold, zinc, selenium, titanium, iron, palladium, cerium, indium, manganese, aluminum, barium, silicon, nickel, zirconium, and their oxides, are used in this regard. Nowadays, it is critical to use nanosystems in conjunction with PTC for mass reproduction, conservation, genetic engineering, crop enhancement, and the synthesis of bioactive compounds. Nanostructured metal oxides play an important role in in vitro plant cultivation. The use of metal nanoparticles (MNPs) has successfully removed microbial contaminants from explants and had a favorable impact on organogenesis (increasing the growth of shoots, roots, and multiplication ratios), callus induction, metabolic changes, and the synthesis of secondary metabolites (NPs are used as elicitors or stress agents). Additionally, NPs cause somaclonal variation (modifications to DNA), improve cryopreservation (increasing the survival rate), and enhance genetic transformation (facilitating gene transformation to bypass the plant cell wall barrier and accelerating protoplast isolation). This review aims to summarize the current breakthroughs achieved by integrating nanotechnology with PTC.

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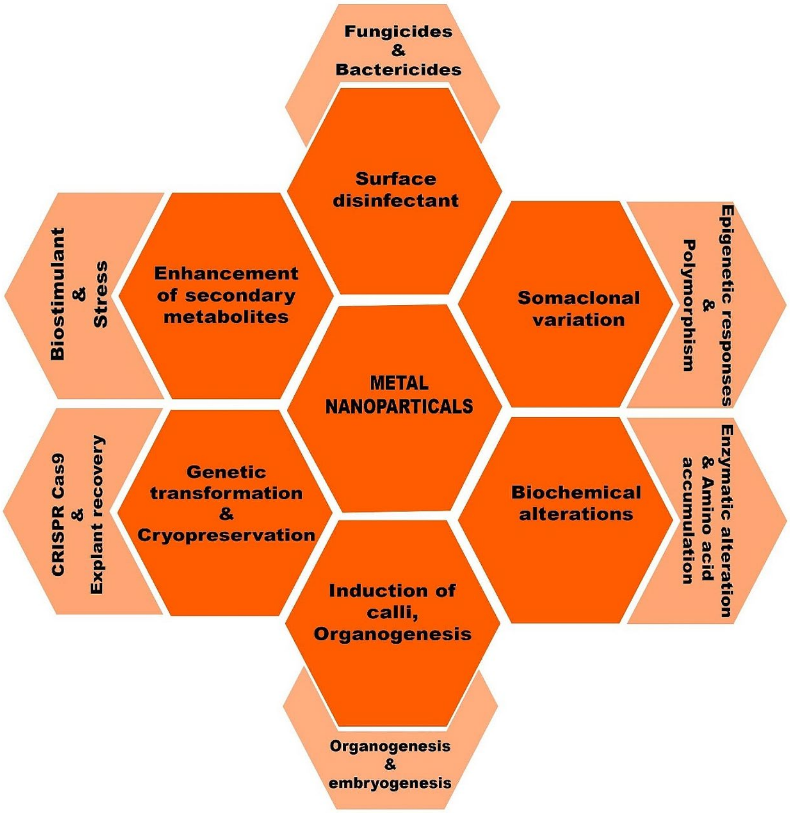
Graphical abstract



Key message

Metal nanoparticles play an important role in in vitro cultures for mass reproduction, conservation, genetic engineering, crop enhancement, and the synthesis of bioactive compounds.

Keywords Secondary metabolites · Metal nanoparticles · Callus induction · Phenolics, *in vitro* plant culture · Genetic transformation

Introduction

The biosphere naturally contains nanoparticles (NPs) due to hydrothermal activity and volcanic eruptions. These particles have a large ratio of relative surface area to volume and at least one dimension smaller than 100 nm (Večeřová et al. 2016). NPs have recently gained significance in many industries including energy, healthcare, environment, and agriculture. Among these, nanomedicine, in particular, is widely accepted as a tool for improving the diagnosis and treatment of human diseases. A wide array of biotechnological instruments could be transformed by nanotechnology, becoming more individualized, less expensive, more portable, safer, and simpler to use. It is possible for poorly soluble, poorly absorbed, and labile physiologically active molecules to be converted into promising deliverable chemicals by means of nanotechnologies (Hasan 2015).

NPs can be synthesized by physical, chemical, or biological (green synthesis) methods. Considering some adverse effects like toxic products production, requirement of specific instrumentation, and economically high expenditure, the biological method is the most convenient, more stable, faster, and eco-friendly alternative. Biological method uses plant extracts, plant wastes, enzymes, algae, fungi and microorganisms (Prasad et al. 2019; Gericke and Pinches 2006). NPs show remarkable properties and vary widely according to their morphology, dimensions, composition, uniformity states, and agglomeration. Metal-, carbon-, composite- and organic-based NPs are examples of nanomaterials (Sengul and Asmatulu 2020).

A shell consisting of either organic or inorganic material or metal oxide often encases the inorganic metal core that forms the basis of metal nanoparticles (MNPs) (e.g., gold, silver, platinum, zinc, iron, etc.) or their compounds (e.g., oxides, sulfides, chlorides, hydroxides, etc.). They are prepared by adding metal salt solution (precursor) to the plant extract (reducing agent). A change in colour is the first indication of the formation of MNPs. NPs characterization can be confirmed using UV-visible spectroscopy, XRD, SEM and TEM. An absorption peak associated to the surface plasmon resonance (SPR) and collective oscillations of conduction band electrons in response to electromagnetic waves can be seen in the UV-visible spectrum of synthesized MNPs, confirming the reduction process and successful synthesis of metallic NPs (Nasrollahzadeh et al. 2019; Piñón-Segundo et al. 2013).

The in vitro aseptic cultivation of cells, tissues, organs, or complete plants under strict environmental controls is known as tissue culture. PTC systems provide a highly controlled and reproducible environment, making them ideal tools for investigating the multifaceted effects of nanoparticles. Clones of plants are frequently created using this technique. The clones produced are true to the genotype that was chosen. Regardless of the season or weather, a single explant can be reproduced into thousands of plants in a very short time and space (Sengul and Asmatulu 2020). In addition to being utilized as a research instrument, PTC approaches have become increasingly significant in the industrial domains of agriculture, horticulture, forestry, plant propagation, disease eradication, crop improvement, and the production of secondary metabolites. This is due to the widespread use of tissue culture technology for large-scale plant multiplication. In PTC, there are several papers that demonstrate the beneficial effects of nanotechnology. Research on crop improvement, plant breeding, commercial plant micropropagation, functional gene studies, the development of transgenic plants with industrial and agronomical traits, the removal of viruses from infected materials to produce healthy, high-quality plant material, the conservation and preservation of genetic resources, and more are some examples of these (Loyola-Vargas and Ochoa-Alejo 2018; Oseni et al. 2018; Tariq et al. 2020).

Reactive oxygen species (ROS), a primary source of toxicity, can be produced by NP exposure, according to both in vitro and in vivo research (Sengul and Asmatulu 2020). In normal plants, ROS is a consequence of aerobic metabolism and is used as a signaling molecule. Nevertheless, when ROS levels rise above a certain point, a range of detrimental consequences known as oxidative stress can occur. These include membrane damage, DNA damage, protein oxidation, electrolyte leakage, and lipid peroxidation, all of which ultimately demolish the cell. (Yang et al. 2017; Fig. 1).

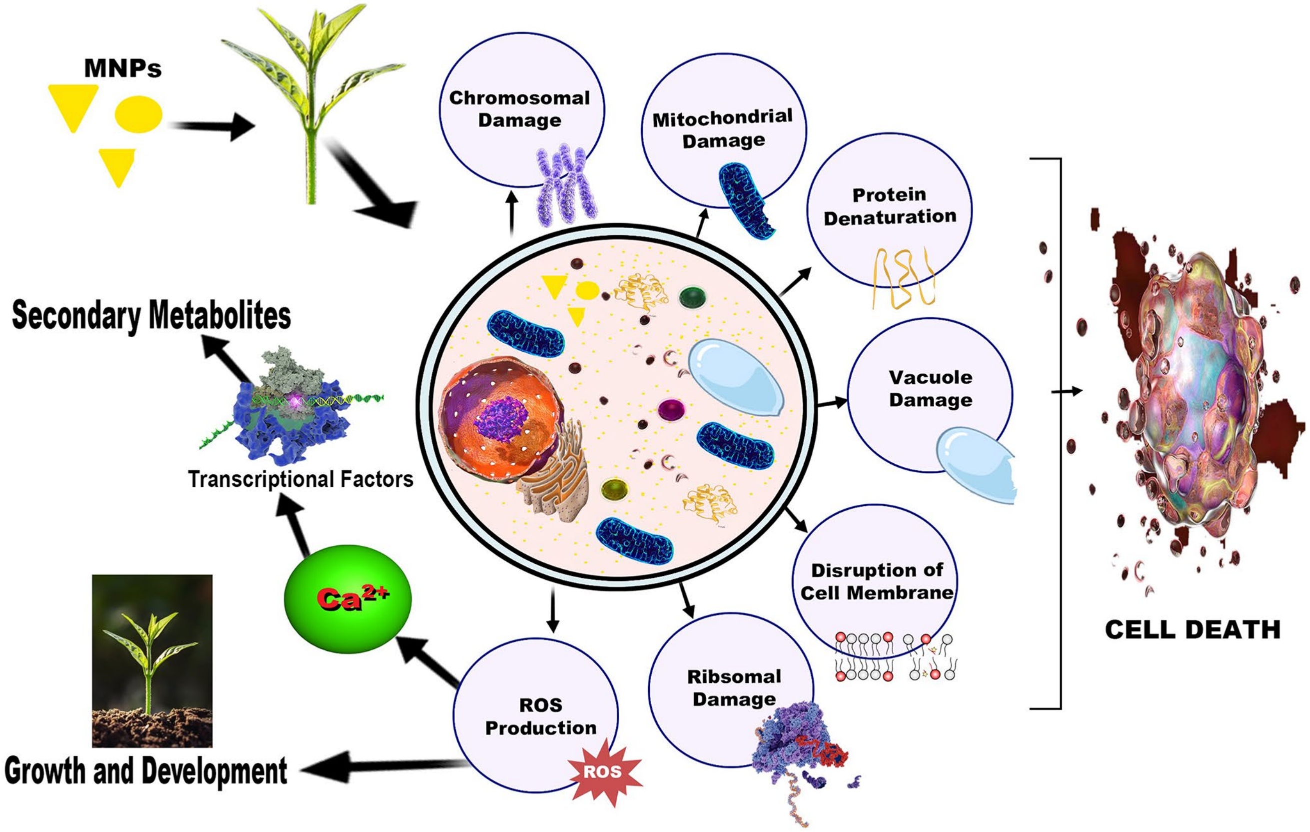


Fig. 1 Toxic and non-toxic effects of MNPs on cells

This article aims to highlight the beneficial properties of MNPs in PTC and to conduct an in-depth analysis to identify the best MNPs currently available for i*n vitro* propagation.

Application of MNPS

Application of nanostructured metal oxides in in vitro plant cultivation ranges from effective removal of microbial contaminants and promoting organogenesis, callus induction, metabolic changes, secondary metabolite synthesis, somaclonal variation, cryopreservation and genetic transformation, thereby enhancing protoplast isolation and cell wall modifications.

MNPS as surface disinfectant and sterilizer

Micropropagation is a highly successful method for producing a large number of plants quickly. It is also useful for plant breeding. However, one of the biggest challenges it faces is microbial contamination, which can lead to the loss of valuable stocks and the lower plant quality. Therefore, the sterilization of culture material is a crucial step in plant micropropagation. Regulators of plant development and the nutritional elements of the culture medium can, regrettably, lose some of their efficacy when exposed to sterilized media. If NP is used as a culture medium ingredient, it can reduce the cost of micropropagation and improve the quality of plants and in addition it acts as a sterilizer (Tung, 2021).

TiO_2NPs are excellent bactericides with an aseptic effect, with no detrimental impact on callus quality (Mandeh et al. 2012). Copper nanoparticles (CuNPs) enhanced the surface disinfection of somatic embryos in tuberous begonias (Begonia x tuberhybrida Voss) in an in vitro study conducted by Bao et al. (2022).

Incorporation of ZnNPs and ZnONPs on growth media at various concentrations can successfully eradicate microbial contaminants in in vitro cultures of Banana with no detrimental effects on regeneration (Helaly, 2014). ZnONPs have been shown to reduce contamination and improve the recovery of *Coffea arabica* leaf explants cultivated in vitro (Devasia et al. 2020). In Murashige and Skoog (MS) media containing 25 mg/L of ZnONPs, the highest explant recovery was seen.

The most harmful endophytic plant-pathogenic fungus, *Colletotrichum gloeosporioides* is responsible for the anthracnose disease that affects many economically significant plants. Through i*n vitro* direct and indirect model systems, bioactive bile salt sodium deoxycholate (NaDC) encapsulated silver nanoparticles (AgNPs) successfully decreased the endophytic fungus with no damage to treated plants (Shanmugam et al. 2015). Another best result was the effects of AgNPs antibacterial activity on the in vitro establishment of the G N15 (almond-peach hybrid) rootstock in comparison to the control group. AgNPs considerably decreased external and internal contaminations whether incorporated into the culture medium directly or via immersion; however, immersion had less of an impact on bacterial and fungal contamination (Arab et al. 2014). After surface sterilization, treatment with 100 mg/L AgNPs solution resulted in the highest percentage of disinfected explants (89%). The characters measured were unaffected by the AgNPs solution.

AgNPs was found to have a high potential for eliminating bacterial contamination from PTC processes. The change of cell membrane structure and function is just one of the any biological processes that silver is known to disrupt microorganisms. Although the precise antibacterial action of silver is poorly known, it also affects the expression of proteins linked to ATP generation. Transmembrane ATP synthesis and ion transport across cell membranes are mediated by the proteins. According to Lok et al. (2006), upon engagement, both AgNPs and Ag (+) ions modify the three-dimensional structure of proteins, beak the disulfide bonds, and obstruct active binding sites, leading to broad functioning issues within the microbe. Another connection between AgNPs' bactericidal action and sugar metabolism blockage has been made. As a result of interacting with AgNPs, the enzyme phosphomannose isomerase (in glycolytic cycle) is rendered inactive and results in diminished sugar metabolism (Bhattacharya and Mukherjee 2008). According to Dakal et al. (2016) study, the AgNP-DNA interaction may result in DNA denaturation or shearing as well as halting division of cells.

The elimination of endogenous and foreign contaminating bacteria is essential for the successful tissue culture of all plants. The two types of microorganisms that are most frequently found in plant tissues are fungi and bacteria. The tobacco tissue culture treated with AgNPs (35 nm) had the same outcomes (Abdi et al. 2008; Safavi et al. 2011a, 2011b; Table 1). When compared to other antibacterial agents, NPs offers long-term residual that is completely safe and works quickly. This technology might significantly reduce the cost of managing plant diseases, and it would undoubtedly enhance profits in the areas where it is used (Shanmugam et al. 2015; Fig. 2).

MNPS in in vitro response of explant, calli, seed, shoot and root

MNPs have garnered considerable interest in agricultural and biotechnological studies owing to their potential utility in PTC, namely in the stimulation of callus formation and organ development (Dikshit et al. 2021; Mohammadinejad

Table 1 Application of MNPs in PTC

No.	Nanoparticles	Role	Plant	References
1.	AgNPs	An increase in survivorship and the average number of new shoots per explant.	*Tecomella undulata*	Aghdaei et al. 2012
2.	AgNPs	Reduce the infestation of phytopathogens, hasten the growth of roots and shoots, and has a great potential for resistance to stress.	*Gray poplar* (Populus × canescens Aiton. Sm.)	Vasyukova et al. 2021
3.	AgNPs	Surface disinfectant.	*Vitis vinifera*	Gouran et al. 2014
4.	AgNPs	Reducing bacterial and fungal contamination in culture medium.	G N15 (almond-peach hybrid)	Arab et al. 2014
5.	AgNPs	Highest seed germination.	*Artemisia absinthium*	Hussain et al. 2017
6.	AgNPs	Proliferation of callus.	*Prunella vulgaris*	Fazal et al. 2016
7.	AgNPs	Production of olefin ethylene, promote explant lifetime and multiplication.	*Tecomella undulate*	Sarmast, 2015
8.	AgNPs	Production of aloin.	*Aloe Vera*	Raei et al. 2014
9.	AgNPs	Stimulate secondary metabolite synthesis.	*Catharanthus roseus*	Shahin 2018
10.	AgNPs	Enhanced antioxidant activity.	*Prunella vulgaris*	Fazal, 2016
11.	AgNPs	Hyperhydricity reversal.	*Dianthus chinensis*	Sreelekshmi et al. 2022
12.	AgNPs	Elevation of proline, protein, carbohydrates, carotenoids, and chlorophyll A and B.	*Phoenix dactylifera*	Elsayh, 2022
13.	AgNPs	Isolation of protoplast.	*Nicotiana tabacum*	Bansod, 2015
14.	AgNPs	Eliminate the adverse effect of Agrobacterium-mediated transformation.	*Tecomella undulate*, *Nicotiana tabacum*	Sarmast and Salehi 2016
15.	AgNPs	Enhance total phenolic, flavonoid content, and high pharmacological activities.	*Momordica charantia*	Chung et al. 2018
16.	AgNPs	Callus proliferation, increased callus biomass, higher production of phenolics, flavonoids and antioxidant activity.	*Caralluma tuberculata*	Ali et al. 2019
17.	AgNPs	Increased production of capsaicin.	*Capsicum frutescens*	Bhat and Bhat 2016
18.	AgNPs	More number of metaxylem.	*Musa acuminata*	Vidyalakshmi et al. 2017.
19.	AgNPs	Elevated production of taxol.	*Corylus avellana*	Jamshidi et al. 2016
20.	AgNPs	Cellular accumulation of bisxanthone, gancaonin O and fusaroskyrin.	*Hypericum perforatum*	Kruszka et al. 2022
21.	AgNPs	Increase survival rate in cryopreservation.	*Pinus radiata*	TPU, 2018
22.	Al2O3 NPs	An increasing effect on physio-biochemical activities such as carotenoid concentrations, chlorophyll a, chlorophyll b, and shoot and root lengths as well as growth attributes including fresh weight, dry weight, and leaf area.	*Hibiscus sabdariffa*	Abdel Latef et al. 2020
23.	Al2O3 NPs	Improved protein, sugar, and pigment concentrations as well as seedling growth.	*Brassica oleracea var. capitata*	Amist et al. 2017
24.	AuNPs	Induced maximum callus proliferation, biomass accumulation, phenolics and flavonoid content.	*Prunella vulgaris*	Fazal et al. 2016
25.	AuNPs	Increase the growth of shoot, roots and multiplication ratio. Plant longevity and quality are increased. The induced metabolic and genetic changes can modify the phenotypics.	*Lamprocapnos spectabilis*	Kulus et al. 2022
26.	AuNPs	Increased secondary metabolite production.	*Artemisia absinthium*	Hussain et al. 2017
27.	AuNPs	Display favorable effects on the development of root and shootlets.	*Gloriosa superba*	Gopinath et al. 2016
28.	AuNPs	Induced hyperxanthone C production.	*Hypericum perforatum*	Kruszka et al. 2022
29.	AuNPs	Improve the cryopreservation efficiency.	*Lamprocapnos spectabilis*	Kulus and Tymoszuk 2021
30.	Carbon-supported AuNPs	Transport DNA.	*Nicotiana tabacum*, *Oryza sativa*, *Leucaena leucocephala*	Vijayakumar et al. 2010
31.	CeO2NPs	Higher accumulation of biomass.	*Arabidopsis thaliana*	Ma et al. 2013
32.	CeO2NPs	Improve biomass and root elongation.	*Glycine max*	López-Moreno et al. 2010a

Table 1 (continued)

No.	Nanoparticles	Role	Plant	References
33.	CeO2NPs	Improve yield.	*Solanum lycopersicum*	López-Moreno et al. 2010b
34.	CeO2NPs	Increased growth and biomass.	*Triticum aestivum*	Rico et al. 2014
35.	CeO2NPs	Enhanced production of emodin anthrone.	*Hypericum perforatum*	Kruszka et al. 2022
36.	Gold-coated mesoporous silica nanoparticles	Transfer DNA and chemicals into the protoplast.	*Tecomella undulata*	Torney et al. 2007
37.	CoNPs	Boost the plant's height, growth index, number of shoots, number of internodes, and reproduction coefficient. increased the output of essential oils.	*Mentha longifolia*	Talankova-Sereda, 2016
38.	CuNPs	Improved the surface disinfection of somatic embryos.	*Begonias* (Begonia x tuberhybrida Voss)	Bao et al. 2022
39.	CuNPs	Height, growth index, number of internodes, number of shoots, and reproduction coefficient should all be increased.	*Mentha longifolia*	Talankova-Sereda, 2016
40.	CuNPs	Increased the percentage of explants that produced somatic embryos as well as the average number of regenerated plantlets.	*Ocimum basilicum*	Ibrahim, 2019
41.	CuNPs	Increased secondary metabolite production.	*Artemisia absinthium*	Hussain et al. 2017
42.	CuNPs and CuONPs	Enhanced production of Apigenin, dihydroxydimethoxyxanthone I	*Hypericum perforatum*	Kruszka et al. 2022
43.	CuONPs	Root induction.	*Stevia rebaudiana*	Ahmad, 2020.
44.	CuONPs	Enhanced effect in growth parameters and nutritive properties at the nano-scale.	*Oryza sativa*	Anwaar et al. 2016
45.	CuONPs	An increase in the overall content of flavonoids and phenols.	*Stevia rebaudiana*	Ahmad, 2020
46.	FeNPs	Better characteristics under harsh situations.	*Fragaria ananassa*	Havas and Ghaderi, 2018.
47.	FeNPs	Increased proline, protein and enzymatic antioxidant activity, reducing the amount of hydrogen peroxide.	*Vitis vinifera*	Mozafari and Ghaderi 2018
48.	FeNPs	Promote root development and seed germination and enhance chlorophyll content.	*Capsicum annuum*, *Solanum. lycopersicum*, *Glycine max*	Ovais et al. 2020
49.	Fe3O4 NPs and Fe2O3 NPs	Create transgenic seeds.	*Gossypium herbaceum*	Zhao et al. (2017)
50.	Fe2O3NPs	Improved seed growth, chlorophyll contents, and gas exchange.	*Triticum aestivum*	Rizwan et al. 2019
51.	In2O3NPs	Increased biomass accumulation.	*Arabidopsis thaliana*	Ma et al. 2013
52.	MnNPs	Promote growth and increase secondary metabolites.	*Atropa belladonna*	Tian et al. 2018
53.	NiONPs	Enhanced expression of genes related to oxidative stress and phenolic compounds	*Brassica rapa ssp. pekinensis*	Chung et al. 2019
54.	PdNPs	Induced production of emodin.	*Hypericum perforatum*	Kruszka et al. 2022
55.	SeNPs	Enhanced organogenesis and root system growth.	*Nicotiana tabacum*	Domokos-Szabolcsy et al. 2012
56.	SeNPs	Increase secondary metabolites, plant productivity and development. Cause Epigenetic response.	*Momordica charantia*	Rajaee et al., 2020
57.	SiNPs	Enhanced plant production and growth in terms of height and chlorophyll content.	*Cucumis sativus*	Alsaeedi et al. 2019
58.	SiO2NPs	Induce somaclonal variation.	*Oryza sativa*	Aboulila and Galal 2019
59.	TiO2NPs	Induced production of quercetin.	*Hypericum perforatum*	Kruszka et al. 2022
60.	TiO_2NPs	Boost callogenesis and calli size.	*Hordeum vulgare*	Mandeh et al. 2012

Table 1 (continued)

No.	Nanoparticles	Role	Plant	References
61.	TiO_2NPs	The seedlings' fresh weight, vigor index, root and shoot length, germination rate index, percentage of germination, and chlorophyll content all showed noticeable improvements.	*Petroselinum crispum*	Dehkourdi and Mosavie, 2013
62.	TiO_2NPs	Production of aloin.	*Aloe Vera*	Raei et al. 2014
63.	TiO_2NPs	Incease in soluble sugars, chlorophyll, carotenoid, and flavonoids.	*Nicotiana tabacum*	Sompornpailin and Chayaprasert 2020
64.	TiO2NPs	Enhance photosynthetic efficiency.	*Spinacia oleracea*, *Solanum lycopersicum*, *Cucumis sativus*	Ovais et al. 2020
65.	Titanium trisulfide nanoribbons	A rhizogenesis-activating agent and as a sterilising agent.	*Betula pubescens x Populus tremula*	Zakharova, 2021
66.	Zn and ZnO NPs	maximum somatic embryogenesis percentage and promoting the regrowth of plantlets with developed root systems.	*Musa x paradisiaca*	Helaly, 2014
67.	ZnONPs	Induction of roots. An increase in both total flavonoid and total phenolic content.	*Stevia rebaudiana*	Ahmad, 2020.
68.	ZnONPs	Positive influence on callus and somatic embryos.	*Coffea arabica*	Devasia et al. 2020
69.	ZnONPs	Callus proliferation, thymol, cravacrol production.	*Thymus vulgaris*	Mosavat et al. 2019
70.	ZnONPs	Increased photosynthetic pigments production.	*Coriandrum sativum*	Pullagurala et al. 2018
71.	ZnONPs	Improved gas exchange, seed growth, and chlorophyll contents.	*Triticum aestivum*	Rizwan et al. 2019
72.	ZnONPs	Induced production of gallic acid.	*Hypericum perforatum*	Kruszka et al. 2022
73.	ZrO_2	Enhance the germination.	*Berberis vulgaris*, *Eruca sativa*	Jalill et al. 2017

et al. 2019). NPs, particularly those comprised of metals have been investigated for their capacity to impact plant growth and development through several processes (Mahendran et al. 2019). MNPs can promote the process of cell division and proliferation in plant tissues, which is essential for the development of calli. NPs, because to their huge surface area and tiny size, may easily enter plant cells and interact with cellular components, hence influencing cellular processes (Giorgetti et al. 2011; Liu et al. 2021). In some cases, the NP can adversely affect the development of the plant segments. For example, the study investigated the impact of various copper oxide (CuO) particles on cell division and gene expression in soybean root tips. It was shown that CuONPs had a strong inhibitory effect on the growth of soybean roots, both in terms of exposure duration and concentration (Liu et al. 2021). But on the other hand, Willow trees exhibit no acute toxicity when exposed to TiO2 NPs and there was no significant impact on growth, transpiration, or water use efficiency during the experiment. These findings indicate that NPs may be advantageous for specific types of plants, detrimental to others, and may have no impact on other species. Response varies based on the characteristics of the NPs and the specific plant it is intended to affect (Seeger et al. 2009). Plant responses to NPs vary widely depending on the NPs' unique properties. The effectiveness of these tiny particles in influencing plants is determined by several factors, including their chemical makeup, size, reactivity, surface coating, and most importantly, the amount applied (Doria-Manzur et al. 2023; Hossain et al. 2015; Khan et al. 2021).

According to research on *Tecomella undulata* (Roxb.) Seem. in vitro propagation, AgNPs' ethylene-blocking impact increased the proportion of explants that produced shoots, the mean number of new shoots per explant, and plant longevity (Aghdaei et al. 2012). Incorporation of ZnNPs and ZnONPs on growth media in banana in vitro culture resulted in the largest percentage of somatic embryogenesis and had the greatest impact on augmenting the regeneration of plantlets with well-formed root systems at 100 mg/L dose (Helaly, 2014). Likewise, ZnONPs had a positive influence on the formation of callus and somatic embryos in in vitro cultivated *Coffea arabica* leaf explants, as explained by Devasia et al. 2020. Root induction is enhanced by the modulatory action of ZnO and CuONPs in MS medium of in vitro produced regenerates of *Stevia rebaudiana* (Ahmad, 2020). Under in vitro conditions, drought stress negatively affected all assessed parameters of strawberry plantlets. Mature embryos of Barley were grown in MS medium with TiO_2NPs suspension and have the potential to greatly boost callogenesis and calli size (Mandeh et al. 2012).

Havas and Ghaderi (2018) treated their plantlets with iron nanoparticles (FeNPs) and salicylic acid (SA) and

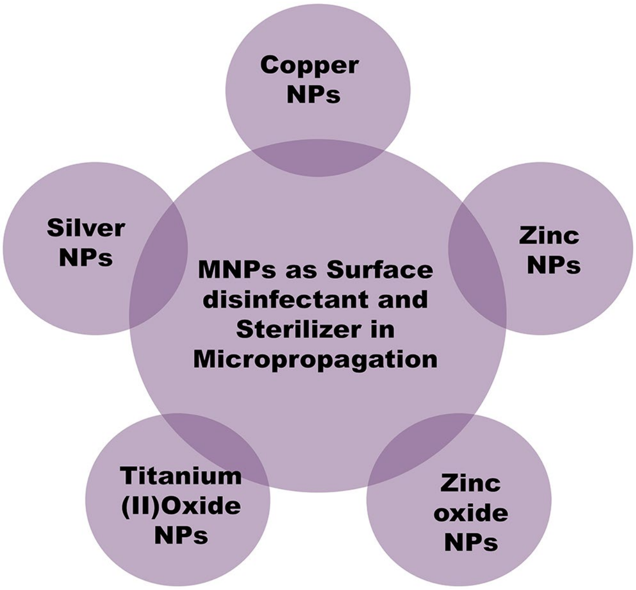


Fig. 2 MNPs as surface disinfectant and sterilizer in i*n vitro*

the result of all parameters of strawberry performed better under harsh situations than untreated strawberry plantlets. Additionally, it had a significant impact on the plantlets' assessed characteristics and growth factors.

The impact of MNPs (Ag, Cu, and Au) in *Artemisia absinthium* seeds that were inoculated on MS medium supplemented with different combinations of MNPs suspension was examined by Hussain et al. (2017) reported that the highest seed germination rates were seen for AgNPs suspensions. In comparison to the application of CuNPs and AuNPs, significant results were found for root length, shoot length, and seedling vigour index (SVI). Both tobacco callus cultures and rooted tobacco plantlets absorbed the red nano-sized elemental selenium (nano Se). Organogenesis and root system growth were promoted by Nano Se (265–530 µM concentration range) (Domokos-Szabolcsy et al. 2012). PTC provides a valuable platform for exploring the intricate influence of AgNPs on plant development. The recently discovered synergy with plant growth hormones offers promising avenues for enhancing plant propagation. When the biosynthesized AgNPs were added to the tissue culture media, they increased the frequency of callus induction, callus renewal, and rhizogenesis. Upon further analysis of the natural hormone levels within regenerating calli, it was shown that the presence of AgNPs improved the process of regeneration by reducing the levels of ethylene and abscisic acid in the plant tissue (Manickavasagam et al. 2019). However, delving deeper into the underlying mechanisms and potential side effects is paramount for responsible and sustainable utilization of this exciting technology.

In *Lamprocapnos spectabilis* 'Valentine,' the growth of shoots and the multiplication ratio are stimulated by the addition of AuNPs to the culture media, particularly at 75 ppm. Further encourage the growth of roots length and its branching (Kulus et al. 2022).

Dehkoudi and Mosavie, (2013) examined the impact of nano priming on parsley germination parameters in tissue culture. The addition of nano-anatase (TiO2NPs) resulted in significant improvements in various growth parameters of seedlings, including germination percentage, germination rate index, root and shoot length, fresh weight, vigour index, and chlorophyll content. The optimal nano-anatase concentration was 30 mg/mL. CuONPs showed a significant effect on plant growth parameters for the regeneration of Oryza sativa and it has the nutritive properties at the nanoscale (Anwaar et al. 2016). When utilised in nutritional mediums during clonal reproduction of *Mentha longifolia*, copper and cobalt NPs boost the plant's shoot quantity, height, internode quantity, growth index, and reproduction coefficient (Talankova-Sereda, 2016).

The effects of single or mixed Au and AgNPs on *Prunella vulgaris* callus growth were examined by Fazal et al. (2016). In comparison to the control, callus proliferation was increased by the Ag, Ag-Au NPs and NAA. When AuNPs were added to the culture medium, the maximum biomass was obtained.

A study by Ibrahim et al. 2019 investigated the effects of CuNPs (20–40 nm) on *Ocimum basilicum* plant regeneration by somatic embryogenesis. The outcomes clearly demonstrated that the addition of CuNPs (5 M) boosted both the average number of regenerated plantlets and the percentage of explants that produced somatic embryos. In PTC, titanium trisulphide nano ribbons have an impact on the downy birch and poplar-aspen hybrid (Table 1). Zakharova, (2021) have discovered that this specific nanomaterial works well both as a sterilising and stimulating agent during the early growth stage and as a rhizogenesis-activating agent during the rooting stage.

Adding 20 mg/L of Cerium oxide (CeO_2) and 50–500 mg/L of Indium oxide (In_2O_3) to ½ MS medium increased biomass accumulation in *Arabidopsis thaliana* (Ma et al. 2013). Studies show that Cerium oxide nanoparticles (CeO_2NPs) enhance root elongation and biomass in Soybeans when exposed to a concentration range of 500–4000 mg/L. CeO_2NPs also significantly improve tomato yield at 10 mg/L. CeO_2NPs alter the nutritional profile and physiology of Wheat and enhance biomass and growth in response to different CeO_2NPs treatments (López-Moreno et al., 2010 (a and b); Rico et al. 2014).

Aluminum oxide nanoparticles (Al_2O_3 NPs) had varied effects on the growth traits and physio-biochemical activities of plants. Abdel Latef et al. (2020) found that a 0.01% concentration of Al_2O_3 NPs had the most significant impact on Egyptian roselle cultivar plants. Similarly, Amist et al.

(2017) reported that lower doses of Alumina NPs improved the growth, pigments, sugar, and protein contents of Cabbage (Brassica oleracea var. capitata) seedlings. Silicon NPs (SiNPs) were studied for their effect on Cucumber plants under water deficit and salinity stresses. Results showed that 200 mg/Kg of SiNPs significantly improved plant growth and productivity in terms of height, chlorophyll content (Alsaeedi et al. 2019). It was reported that Zirconia (ZrO_2) nanoparticles can enhance the germination of *Berberis vulgaris* and *Eruca sativa* (Jalill et al. 2017).

FeNPs and TiO_2NPs have positive effects on plant growth, depending on their concentration. Low concentrations of Iron oxide nanoparticles promote root development and seed germination and enhance chlorophyll content in certain plants, such as *Capsicum annuum*, *Solanum. lycopersicum*, and Soybeans. TiO_2NPs enhance photosynthetic efficiency in *Spinacia oleracea* L., *S. lycopersicum*, and *Cucumis sativus* plant species (Ovais et al. 2020). ZnONPs or Fe_2O_3NPs priming for 24 h improved wheat seed growth, chlorophyll contents, and gas exchange. ZnONPs also reduced lipid peroxidation and increased photosynthetic pigments in *Coriandrum sativum* (Rizwan et al. 2019; Pullagurala et al. 2018).

MNPS on enhancement of secondary metabolites

All plants produce secondary metabolites, which are challenging to extract and purify since they are frequently unique to a single species or genus under particular environmental conditions. Since ancient times, secondary metabolites have been important in medicine. The poor output of metabolites is a significant barrier to the manufacture of secondary metabolites using plant cell culture technologies (Ramachandra-Rao & Ravisankar, 2002; Shilpa et al. 2010). One of the main methods for increasing the supply of secondary metabolites has been the use of elicitors in cell cultures. As per recent investigations, MNPs may be employed as a potential elicitor to boost the synthesis of bioactive plant metabolites, (Radman et al. 2003; Rivero-Montejo et al. 2021).

Elicitors can be abiotic stressors and biostimulants, which are products that are designed to enhance plant nutrition, production, and other aspects. Stress is the main trigger for plants to release active secondary metabolites, and a range of elicitors can mimic stress by triggering the plant's active chemical defenses. ROS and secondary signalling messengers that result in transcriptional control of plant secondary metabolism have been suggested by specific authors as being induced by NPs. Significant second messengers (ROS and calcium ions (Ca2+) that cause the up-regulation of transcriptional regulators of secondary metabolites (Rivero-Montejo et al. 2021; Anjum et al. 2019; Marslin et al. 2017; Fig. 1).

Plants when exposure to NPs, which can induce complex physiological and biochemical responses. NPs such as Ag, ZnO, Al_2O_3, etc., induce ROS production in plants through various mechanisms. Upon NP exposure, ROS like hydrogen peroxide (H_2O_2) and superoxide anion (O_2^-) accumulate due to NADPH oxidase activation at the plasma membrane. This oxidative burst triggers downstream signaling pathways involving mitogen-activated protein kinases (MAPKs), which regulate gene expression for defense responses (Humbal et al., 2023, Thwala et al. 2013; Zhao et al. 2012).

Arabidopsis thaliana root hair defective 2 mutant lacking NADPH oxidase (RBOH) exhibited a considerably lower amount of ROS formation in response to AgNPs. This suggests that the enzymes that make ROS at the apoplast, which are attached to the plasma membrane, are responsible for mediating the accumulation of ROS in cells (Sosan et al. 2016; Mittler 2017). However, based on AgNPs' ability to block Ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activity and PSII's potential for photoprotection, Chloroplastic ROS production was seen in *Spirodela polyrhiza* (Jiang et al. 2017). According to Jiang et al. (2017), ions released from NPs rather than intact particles are the source of ROS activation. Internalized silver (Ag) in *S. polyrhiza* has the same potential to produce ROS whether it comes from exposure to Ag ions or AgNPs. Likewise, other studies have demonstrated that ZnO, CuO, and CeO_2 dissolve into the corresponding ions (Zn^{2+}, Cu^{2+}, Ce^{4+}) (Ebbs et al. 2016; Bradfield et al. 2017).

Additionally, the ion balance of plant cells was disturbed by NP exposure. NP-induced stress responses depend critically on Ca^{2+} influx and efflux, which are mediated by channels and pumps. Increased levels of cytosolic Ca^{2+} stimulate a number of signaling pathways and transcription factors, affecting the expression of genes linked to the generation of secondary metabolites and stress adaption (Sosan et al. 2016). Plants utilize both non-enzymatic (glutathione) and enzymatic (superoxide dismutase, catalase, and ascorbate peroxidase) antioxidant mechanisms to counteract oxidative damage caused by NPs. These systems are essential for cellular survival and function under stress because they detoxify ROS and preserve redox balance inside cells (Sewelam et al. 2016; Tripathi et al. 2017).

According to previous research, NPs may regulate plant secondary metabolism and interfere with signalling pathways. The specific mechanism of this modulation is still unknown. It is believed that early plant responses to NP exposure may involve elevated levels of reactive oxygen species (ROS), cytoplasmic calcium (Ca^{2+}), and activation of mitogen-activated protein kinase (MAPK) cascades.

Molecules that are important to cells, like proteins, DNA, and lipids, can be harmed by excessive ROS production in reaction to NPs. According to Van Breusegem and Dat (2006) and Faisal et al. (2016), this damage compromises the integrity of the membrane, hampers the function of organelles, and may result in programmed cell death. Chromosomal abnormalities, DNA fragmentation, and mutagenesis are genotoxic consequences they cause in plants. According to Kumari et al. (2009) and Rajeshwari et al. (2016), these impacts hinder plant growth and development and demonstrate the potential for NPs to be cytotoxic in some situations.

The most significant secondary metabolite in *Aloe vera* L is called Aloin. The findings demonstrated that nano silver (NS) treatment of aloe suspension cell cultures caused the Aloin content to rise to 43.7% in 48 h following treatment before progressively declining and reaching the control level. A 48 h Nano-Tio2 treatment produced the most Aloin, which was reduced to a lower level at 168 h (Raei et al. 2014). The modulatory effect of CuONPs (up to a 20 mg/L dosage) and ZnONPs (up to a 2 mg/L dosage) applied to the MS culture medium of in vitro grown regenerants of Candy leaf noticeably triggered biochemical profiling. Total phenolic, total flavonoid content, steviol glycosides concentration and 2,2-diphenyl-1-picryl hydrazyl-free radical scavenging activity were calculated to be the highest (Ahmad, 2020). MNPs, specifically Ag, Cu, and Au, showed an increased secondary metabolite production, total phenolic and flavonoid content, antioxidant, superoxide dismutase (SOD) activity, and total protein content (Hussain et al. 2017). Copper and Cobalt NPs intensified the essential oil production in *Mentha longifolia* (Talankova-Sereda, 2016). Likewise, AgNPs as the elicitor that can induce the production of secondary metabolites of *Catharanthus roseus* L., which incite defence responses. The high content of vinblastine was seen in those explants treated with 75 mg/L AgNPs (Shahin 2018). The transcription factor WRKY1 in *Momordica charantia*, which is involved in secondary metabolism and growth regulation, was upregulated as a result of the administration of nano Se to the culture medium. These can boost the immune system, development and plant productivity (Rajaee et al., 2020). The Ag-AuNPs, in combination with NAA induced maximum accumulation of phenolics and flavonoid content. Moreover, Ag-AuNPs without NAA enhanced antioxidant activity in *Prunella vulgaris* (Fazal, 2016; Table 1).

According to Oukarroum et al. (2013), AgNP phytotoxicity was mediated by ROS generation because there was a strong association between the reduction in viable cells and ROS generation at doses of Ag NPs up to 10 mg/mL over the course of a week-long treatment period. Lin and Xing (2008) suggested that lipid peroxidation and particle-dependent ROS production took place on the surface of cellular membranes of ryegrass due to ZnONP phytotoxicity.

Cell cultures of *H. perforatum* were exposed to Ag, Au, Cu, Pd, CeO_2, CuO, TiO_2, and ZnO NPs to study the changes in secondary metabolism. Among the NPs tested, Ag and CuO induced the most significant changes. Ag NPs caused the cellular accumulation of bisxanthone, gancaonin O and fusaroskyrin. Other NPs induced the following compounds the most: hyperxanthone C (Au), apigenin (Cu), emodin (Pd), emodin anthrone (CeO_2), dihydroxydimethoxyxanthone I (CuO), quercetin (TiO_2), and gallic acid (ZnO). Therefore, the types of NPs have varying effects on the secondary metabolites elicitation (Kruszka et al. 2022).

Manganese (MnNPs) NPs is a less explored NP. Mn_2O_3 NPs, at a concentration of 25 mg/L, promote growth and increase secondary metabolites in in vitro culture of *Atropa belladonna* plants by activating antioxidant enzymes (Tian et al. 2018). Exposure of *Corylus avellana* cell suspension culture to 5 mg/L Ag NPs significantly increased taxol production (Jamshidi et al. 2016). The biosynthesized Barium (BaONPs) NPs have shown strong antibacterial, antioxidant, and anti-inflammatory properties, making them a promising candidate for future therapeutic use (Abdullah, et al., 2023).

The application of NPs in medicinal plants as a method to boost biological activity without phytotoxicity was demonstrated by current research as a way to promote the manufacture of bioactive chemicals. However, further research is required on the possible impacts of using nanomaterials as an elicitor on ecosystems and human risk (Rivero-Montejo et al. 2021).

MNPS as biochemical alterations

The enzyme 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, a pivotal enzyme in the biosynthesis of the simplest olefin ethylene, is significant in in vitro culture conditions and can modulate many facets of the plant life cycle. Transgenic plants with altered ethylene levels, such as tomatoes, can be produced by using ACC synthase and ACC oxidase, which silences the expression of endogenous genes, resulting in slow ripening fruits due to very low levels of ethylene. (Arshad and Frankenberger 2012). In in vitro MS medium with AgNPs may promote explant lifetime and multiplication in regenerated *Tecomella undulate* (Roxb.) Seem. leaves, enhancing survival and delayed explant senescence, according to gene expression patterns of acetyl-CoA synthetase (ACS) gene. (Sarmast and Salehi, 2015). When exposed to saline stress, grape softwood cuttings cultures treated with potassium silicate and iron nanoparticles may significantly increase total protein and free proline levels as well as enzymatic antioxidant activity, hence lowering hydrogen peroxide levels. Iron and potassium silicate has been demonstrated to boost potassium levels and decrease sodium content when exposed to salinity stress. The results of this study suggest that the use of micronutrients in stressful situations is a practical and effective strategy to mitigate the negative effects of saline stress (Mozafari and Ghaderi 2018). Bleeding heart's metabolite profile is altered by *Lamprocapnos spectabilis* 'Valentine' in medium-temperature cultivation with AuNPs, and acclimated plants' longevity and quality were increased (Kulus et al. 2022). One of the most significant issues in PTC is hyperhydricity (HH). The use of biogenic AgNPs greatly decreased the proportion of HH in MS medium cultures of *Dianthus chinensis* because of the biological activity of Ag + ions and water controlling mechanisms. Also successfully decreased the amount of hydrogen peroxide (H_2O_2). The genetic stability of AgNPs-directed HH reversed shoots was observed (Sreelekshmi et al. 2022). The physiology of tobacco plants, including their levels of total soluble sugars, chlorophyll, carotenoid, and flavonoids, was reported to be improved using 20 mg/L of TiO_2 NPs in comparison to untreated controls (Sompornpailin and Chayaprasert 2020). Carotenoids, Chlorophyll A and Chlorophyll B are increased in the date palm cultivar Hayani's culture medium when 3.0 ml/L AgNPs are present. Additionally, the proline, protein, and carbohydrate contents have all increased (Elsayh, 2022; Table 1). The nutraceutical business can profit from metallic oxide NPs as they can improve the generation of bioactive metabolic components from medicinal plants in in vitro batch cultures. (Ahmad, 2020). Nickel oxide NPs (NiONPs) exposure on Chinese cabbage led to enhanced expression of genes related to oxidative stress and phenolic compounds (Chung et al. 2019).

MNPS on somaclonal variation

For every micropropagation system, the development of somaclonal variation is a major subject of concern. The term "somaclonal variation" refers to phenotypic and genotypic differences brought by tissue culture. Kokina et al. 2017 investigated how Linum usitatissimum's somaclonal variation was impacted by Au and AgNPs. Both calli and regenerants grown on media containing Au and AgNPs had a higher incidence of somaclonal variation. Au and AgNPs use in tissue culture has expanded recently, although it's still unclear how nanoparticles cause modifications to the DNA. When used in high amounts, AuNPs (a substance that acts as a mutagen) can cause genetic diversity. The induced metabolic and genetic changes can modify the phenotypic characteristics of *Lamprocapnos spectabilis*, resulting in the development of new cultivars (Kulus et al. 2022). Through cytosine DNA methylation, nanoSe supplementation in bitter melon was linked to an epigenetic response, and the treatments elevated genes like PAL and 4-coumarate: CoA-ligase (4CL) (Rajaee et al., 2020). The DNA changes and mutations in four rice genotypes caused by SiO_2NPs were analyzed and somaclonal variations using RAPD and SSR analyses. Genotype significantly affected callus induction and plant regeneration. The genome template stability percentage (GTS%), reflecting changes in Random amplified polymorphic DNA (RAPD) profiles (DNA based techniques used to evaluate the variation at the DNA sequence level), was the most sensitive endpoint. Two SSR markers generated polymorphism, aiding in rice plant breeding for drought tolerance (Aboulila and Galal 2019; Table 1).

MNPS on genetic transformation

Plant genetic engineering, a modern innovation in plant science, is a significant tool for enhancing yield, crop quality, secondary metabolite levels in medicinal plants, and cultivating crops suited for sustainable agriculture (Cardoso et al. 2019; Niazian 2019). MNPs can augment the efficacy of genetic transformation in plants by facilitating the absorption and incorporation of exogenous DNA into plant cells (Cunningham et al. 2018).

A new method using NPs for plant gene transformation accurately transports DNA or RNA, enabling transient or stable transformation. NP-mediated gene transformation gets around the barrier of the plant cell wall (Lv, 2020). This process can result in transgenic plants possessing advantageous characteristics, which can be valuable for enhancing crop quality. A novel method utilizing nanoparticle-mediated gene transformation offers a solution to the challenge posed by the plant cell wall, facilitating precise delivery of DNA or RNA into plants to produce transient or stable transformation (Lv et al. 2020; Mali et al. 2020). For the delivery of nucleic acids in plant cells, several nanomaterials such as mesoporous silica NPs, magnetic NPs, carbon nanotubes, etc., have been used recently (Jat, 2020).

Secondary metabolite levels have increased due to recent advances in plant genetic engineering (Lv et al. 2019). Plants may now efficiently receive DNA or RNA through the use of nanoparticles, circumventing the plant cell wall and enabling either transient or permanent genetic modifications. Nanoparticle-based gene transformation is widely used in animal cells, but it is still in its infancy when it comes to plants (Billingsley et al. 2020; Lv et al. 2020). Growing capabilities in genetic engineering have made it possible for scientists to precisely target particular plant gene regions for desired molecular changes (Cunningham et al. 2018). Many molecular techniques are used to accomplish this; among them is the recently developed CRISPR-Cas9 (Cluster regularly interspaced short palindromic repeat (CRISPR)-associated protein 9) method, which provides more precision than the others. Because of its precise gene-editing abilities, CRISPR offers researchers a valuable tool to improve the production of significant natural products by allowing them to change specific genes involved in biosynthetic processes (Sidhic et al. 2024). Scientists are intrigued by the prospect of delivering the CRISPR system, which does away with the need for viruses through nanoparticles (Cunningham et al. 2018). Different approaches have been investigated to introduce nanoparticles into plant cells. These include combining distinct CRISPR/Cas9 variants with different kinds of nanoparticles, including nanocapsules, gold nanoparticles, hydrogels, peptide-based nanoparticles, DNA nanoclew, polymeric nanoparticles, magnetic nanoparticles, and nanocapsules. By serving as carriers, these nanoparticles make it easier for target genes to enter host cells. These nanoparticles can be absorbed by plants to modify the target gene sequence in a precise way (Vats et al. 2022). Compared to animal cells, plants have diverse cellular architecture and complex cell walls, which pose special problems for nanoparticle-based gene delivery (Peng et al. 2022). Further research is required to optimise nanoparticle-based gene delivery methods for plants, addressing the issues while improving the efficiency and reliability of genetic alteration approaches.

Magnetofection is a drug delivery method using magnetic NPs to transfer genes into the cell nucleus. Magnetic Fe_3O_4 and Fe_2O_3 NPs are ideal for various applications due to their thermal stability, large surface area, small size, stability and low toxicity (Lv et al. 2020). Zhao et al. (2018) created a method that uses magnetic NPs to create transgenic seeds. A magnetic field was used to push the plasmid DNA into the pollen after it had been enclosed in magnetic NPs. The resulting transgenic cotton generated seeds with stable inheritance of the transformed DNA.

Research on plants can benefit from leaf protoplast isolation. Standard reference techniques for isolating protoplasts are laborious, damaging cells, generating minimal amounts of material, time consuming, and are prone to microbial contamination. The addition of 10 mg/L AgNPs to leaf incubation buffer during protoplast isolation produced 3 h of protoplast isolation that produced 34% viable protoplasts. This is the first account of the manufacture of AgNPs from used plant media, which was used to sterilize explants and quickly isolate protoplasts (Bansod, 2015). Through the use of a gene gun, Vijayakumar et al. (2010) showed that carbon-supported AuNPs can transfer DNA into plants such as *Nicotiana tabacum*, *Oryza sativa*, and *Leucaena leucocephala* with minimal damage to the cells and with less gold and plasmid, thus encouraging plant regeneration and transformation frequency. The authors Torney et al. (2007) demonstrated how mesoporous silica NPs may be used to transport DNA into tobacco protoplasts by endocytosis. They achieved this by utilizing gold-capped mesoporous silica NPs to deliver DNA and chemicals into the callus and leaves using a biolistic gun. Antibiotics used in Agrobacterium-mediated transformation can negatively impact the regeneration potential and genetic stability of regenerated plantlets due to their phytotoxic effects on explants. According to Sarmast and Salehi (2016) *Agrobacterium tumefaciens* and *A. rhizogenes* growth was entirely inhibited on LB medium with AgNPs. The scientists also showed that the co-cultivation of *Tecomella undulata* and tobacco with Agrobacterium led to the successful elimination of bacteria with the addition of AgNPs to the culture medium (Table 1).

MNPS on cryopreservation

The process of preserving plant genetic resources for the long term by storing cell lines, tissues, organs, calli, etc., at a temperature of liquid nitrogen (-196 °C) is called cryopreservation (Kaviani 2011). The addition of NPs to the cryoprotectant process can improve thermal conductivity and viscosity, induce vitrification, suppress devitrification, and enhance solution stability during rewarming (Wang et al. 2015). The unique thermal properties of NPs have significant potential in cryobiology, such as preventing the formation of ice crystals at temperatures below zero (Hou et al. 2018). In addition, NPs also maintain the recovery potential of explants upon introduction to the plant tissue culture medium, protective bead matrix, or to the recovery medium (Tymoszuk and Miler 2019).

The culture medium and preserving medium of *Pinus radiata* embryogenic cell lines were supplemented with Ag NPs and stored at -80 °C, resulting in a 75% recovery rate (TPU, 2018). Researchers used in vitro-derived shoot tips of *Lamprocapnos spectabilis* ‘Valentine’ and cryopreserved them with AuNPs added either into the preculture medium, the protective bead matrix, or the recovery medium. The study found that adding 10 ppm of AuNPs into the alginate bead matrix improved the recovery level of LN-derived shoot tips (70.0%) compared to the non-NPs-treated cryopreserved control (50.5%). However, adding nanoparticles to the recovery medium had a negative effect on the survival of explants. Moreover, adding AuNPs affected the enzymatic activity in *L. spectabilis.* Adding AuNPs at a lower concentration (10 ppm) into the protective bead matrix can significantly improve the cryopreservation efficiency in *L. spectabilis* without altering the DNA sequence (Kulus and Tymoszuk 2021). There is currently limited information available on the use of NPs in the cryopreservation of plant material.

Conclusion and future prospects

The burgeoning field of nanotechnology with PTC has opened a plethora of promising applications, including mass reproduction, conservation, genetic engineering, crop enhancement, and bioactive compound synthesis. Nanostructured metal oxides have emerged as particularly crucial in in vitro plant cultivation. MNPs have demonstrated remarkable efficacy in removing microbiological pollutants from explants and positively influencing various processes, such as organogenesis, induction of callus, metabolic alterations, synthesis of secondary metabolites, somaclonal variation, and genetic transformation.

Looking towards the future, further research in this area holds immense promise for addressing global challenges in food security, environmental sustainability, and human health. Continued exploration of green NP synthesis methodologies could lead to the development of novel and more efficient techniques, paving the way for wider adoption of green NPs in various applications. Delving into the mechanisms governing NP-plant interactions will deepen our understanding of how nanomaterials can effectively enhance productivity, plant growth and stress tolerance. Extensive research is required to clarify the long-term consequences of MNPs. on plant development, soil health, and ecosystem dynamics, ensuring their sustainable use in agricultural practices. Additionally, exploring innovative methods for delivering MNPs to specific plant tissues or organelles could unlock new avenues for targeted manipulation of plant physiology and metabolism. In conclusion, the future prospects of nanotechnology in plant science hold immense potential for addressing pressing global issues and shaping a more sustainable and prosperous future. By harnessing the synergistic power of green nanotechnology and PTC, we can revolutionize agriculture, enhance food security, and contribute to the well-being of humanity in various dimensions by addressing the United Nations Sustainable Development Goal 3- Good Health and Well-being.

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