Research Article

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Nanomaterials: Cross-disciplinary applications in ornamental plants

https://doi.org/10.1515/ntrev-2024-0049
received October 27, 2023; accepted June 7, 2024

Abstract: Nanomaterials (NMs) have found extensive applications in the realm of ornamental plants due to their unique properties. This article comprehensively discusses four main aspects of NM utilization in ornamental plants: 1) providing new insights into challenging problems in tissue culture, 2) exploring their regulatory effects on the growth of ornamental plants, 3) enhancing the resistance to biotic and abiotic stressors, and 4) discussing their widespread application and mechanisms in cut flower harvesting. Furthermore, potential issues and future directions are explored, providing a deeper theoretical basis for the application of novel NMs in the realm of ornamental plants.

Keywords: NMs, ornamental plants, postharvest physiology, stress resistance, tissue culture

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1 Introduction

Ornamental plants play an essential role in horticulture, not only to bestow upon individuals the joys of beauty visually and spiritually, but also create economic and ecological value. With the rise in living standards, the demand for ornamental plants has steadily increased. However, ornamental plants frequently encounter challenges during their cultivation and production. First, processes such as rapid plant propagation, virus elimination, the cultivation of new plant varieties largely rely on tissue culture. Yet, the establishment of tissue culture systems is impeded by issues like microbial contamination, browning, and vitrification [1]. Second, during growth horticultural plants may face various biological and abiotic stresses. In addition, postharvest management of horticultural plants often involves bacterial contamination and the aging of cut flowers during preservation [2]. These challenges not only harm the plants but also constraint the ornamental plant industry. To address these issues, a comprehensive application of multidisciplinary technological achievements is required, of which, the nanometer materials as an emerging technological tool, is being used in the fundamental research and production of ornamental plants.

Nanometer is fundamentally a unit of length measurement, regardless of whether in a gaseous, liquid, or solid state, with particle sizes typically falling within the range of 1–100 nm [3]. Nanomaterials (NMs) primarily encompass metal nanoparticles (NPs), nonmetallic NPs, carbon nanotubes, nanocrystalline quantum dots (GQD), polymer micelles and polymer NPs. At the nanoscale, the number of surface atoms, surface area-to-volume ratio, and particle energy rapidly increase, endowing NMs with unique nanoscale effects, including surface effects, small size effects, quantum effects, and macroscopic quantum tunneling effects [4]. These properties render NMs of wide-ranging value in various fields such as physics, chemistry, biology, and healthcare [5,6]. As a vital branch of biology, plants hold significant importance for both the natural environment and human life. Since the early twenty-first century, NMs have been employed in plant research. Studies have revealed that when the particle size of NMs is less than 10 nm, they can enter plant cells directly through cell wall pores, plasma membranes, or ion channels [7]. When the NMs have particle sizes larger than 10 nm, they can be transported into plant cells through phagocytosis or active transport [8]. NMs can be used as growth regulators, antimicrobial agents, herbicides, insecticides, and fertilizers [5,6]. They can also exert influence on plants through mechanisms like targeted protein transport, biosensors, and nanosimulants. Consequently, NMs possess the potential to enhance plant growth [9].

In recent years, significant progress and innovations have been made in the field of NMs to address the challenges of sustainable agricultural production and food security. NMs hold the potential to promote plant growth and protect crops and are currently widely employed in agriculture, greatly enhancing efficiency and productivity [10]. While substantial achievements have been realized in agricultural applications such as plant protection, crop nutrition, and farm management [11], research in the context of ornamental plants is still in early stages. The application of NMs in the field of horticultural plants primarily encompasses aspects related to plant growth and development, genetic transformation, and plant health [12]. This article provides an overview of the application of NMs in ornamental plants, with a particular focus on four key areas: tissue culture, cultivation and growth, stress resistance, and post-harvest physiology. This emphasizes the potential of NMs in the realm of ornamental plants.

2 Application of NMs in ornamental plant tissue culture

Tissue culture is not only a crucial means of rapidly propagating plants but also plays a significant role in various areas, including asexual reproduction, virus-free seedling cultivation, breeding new varieties, artificial seeds, and genetic resource preservation [13]. Additionally, it serves as the foundation for plant genetic engineering and breeding. Some metal NMs have been demonstrated to have an impact on the process of tissue culture in ornamental plants, such as inhibiting microbial growth, alleviating plant hyperhydration, and promoting plant regeneration. Among these, research on nano-silver (NS) is the most extensive, and materials like ZnO NP and nano-gold (NG) also have certain effects on the regeneration of tissue-cultured ornamental plants (Table 1).

2.1 NS is the main material applied in ornamental plants and has excellent effects

The key to successful plant tissue culture lies in effectively addressing both exogenous and endogenous microbial contamination and managing excessive water content in plant materials. The use of NS has introduced a fresh approach to tackling these issues. Research indicates that silver can interact with thiol (–SH) groups in microbial proteins and the bases in DNA, adversely affecting bacterial respiration [22]. Consequently, silver and its compounds have been employed as antimicrobial agents for an extended period [23]. With the advent of NMs, researchers have discovered that smaller-sized NS, even at low concentrations, exhibit remarkable antibacterial, antifungal, and antiviral properties [24].

Table 1: Applications of metal NMs in the culture and propagation of ornamental horticultural plants

NMs	Species	Application type	Ref.
NS	*R. hybrida* L.	Bacterial contaminants	[14]
NS	*L. brownii* var. *viridulum* Baker	Bacterial contaminants	[15]
NS	*C. morifolium* Ramat.	Water microponics	[16]
NS	*D. chinensis* L.	HH reversion	[17]
NS	*C. morifolium* Ramat.	Genetic, biochemical, and phenotype variation	[18]
NS	*C. morifolium* Ramat.	Regeneration, genetic, biochemical, and phenotype variation	[19]
ZnO NMs	*L. brownii* var. *viridulum* Baker	Phenotype variation, secondary metabolite production	[20]
NS, NG	*C. morifolium* Ramat *G. jamesonii* Bolus *Streptocarpus* × *Hybridus*	Plant growth	[21]

Shokri *et al.* pioneered the application of NS in the tissue culture of ornamental plants. Their groundbreaking work revealed that the addition of 100 ppm NS to the culture medium effectively reduced bacterial contamination and phenolic leakage in *Rosa hybrida* stem segments during the tissue culture process [14]. Moreover, the antibacterial effect of directly adding NS to the culture medium outperformed immersion treatments. However, it should be noted that high concentrations of NS could inhibit the growth of rose stem segment [14]. Subsequently, Gioi *et al.* found that using 300 ppm NS to lily (*Lilium brownii* var. *viridulum* Baker) bulbs not only effectively sterilized them *in vitro* but also stimulated the morphological growth. On a culture medium containing 4 ppm NS, the highest bulb scale formation coefficient was observed, while adding 6 ppm NS resulted in the highest bulb rooting rate [15]. The vast surface area of tiny NPs endows them with remarkable antimicrobial properties by interfering with the respiration, growth, and reproduction of microorganisms [25]. Based on the antibacterial performance of NS, Tung *et al.* applied them to the micropropagation system of *Chrysanthemum morifolium*. They found that under 70% red light and 30% blue light LED irradiation, the addition of 7.5 ppm NS to the culture medium significantly enhanced the growth rate of shoots and effectively reduced the microbial counts of eight bacterial species and three fungal species. This further confirmed that NS not only inhibits microbial growth but also promotes the growth of tissue-cultured plants. However, it is worth noting that further increasing the concentration of NS, while improving the inhibitory effect on microorganisms, did not favor the growth conditions of *Chrysanthemum*, leading to the deformation and death of some leaves [16].

In summary, in tissue culture of different ornamental plants, the addition of an appropriate concentration of NS can inhibit microbial growth, but the sensitivity of different microorganisms to NS is influenced by factors such as concentration, exposure time, and treatment methods. Although a higher NS concentration results in better microbial inhibition, it may to some extent affect the regeneration rate of explants and even cause damage to them. Therefore, when applying NS, it is necessary to choose the appropriate NS concentration and control the treatment time according to the specific tissue characteristics of different ornamental plants to achieve effective inhibition of microbial growth.

In addition to microbial contamination, hyperhydricity (HH) is also one of the main issues in plant tissue culture, leading to the development of unhealthy, pale, and glassy new shoots. NS have also played a positive role in addressing the problem of HH. Research has shown that there is an interaction between ethylene and HH, and the abnormal accumulation of ethylene under *in vitro* conditions and imbalanced water content inside the plants is the main cause of high water content. Silver ions can interfere with ethylene synthesis by binding to ethylene signal transduction receptors, thereby preventing HH [26,27]. Based on this characteristic, a study by Sreelekshmi *et al.* found that using biologically synthesized NS to treat hyperhydric *Dianthus chinensis* significantly reduced content of the relative water and the hydrogen peroxide content in the plants. Compared to plants suffering from HH, those treated with NS showed a significant reduction in the expression of ethylene synthesis key enzyme genes ACS1 and ACO1 in the plants. Simple sequence repeat analysis of the HH regenerative shoots treated with NS showed genetic stability, confirming the low toxicity of NS [17]. This study provides strong reference for the use of NS as an anti-ethylene agent in alleviating HH issues in plant tissue culture (Figure 1).

Furthermore, NMs can be utilized as a novel chemical mutagen added to the culture medium. Compared to physical mutagens such as gamma rays, X-rays, and ultraviolet light, this method is simpler and more feasible, requiring no complex equipment [28].

Currently, among ornamental plants, only NS have been applied as mutagens in the *in vitro* propagation of *Chrysanthemum*. Tymoszuk and Kulus found that 50 and 100 mg/L of NS could suppress the formation of adventitious buds in leaf explants and the efficiency of bud regeneration [18]. This inhibition affected the biosynthesis of primary and secondary metabolites and also influenced the activity of the antioxidant enzyme defense system. Furthermore, during *in vitro* cultivation, they identified *Chrysanthemum grandiflorum* "Lilac Wonder" exhibited a color change from pink to purple-red [18]. Therefore, NS may possess epigenetic effects, resulting in changes in DNA methylation or acetylation.

Subsequently, Tymoszuk and Kulus found that added 20 ppm of AgNPs, induced the regeneration of intermodal shoots in "Lilac Wonder" [19]. Polymorphic loci were detected in 12 and 9 of the NS-treated plants using random amplified polymorphic DNA and inter-simple sequence repeat markers, respectively. Phenotypic changes were observed in six plants, including alterations in pigment content (anthocyanin and carotenoids) and inflorescence shape, with only two plants exhibiting both genetic and phenotypic polymorphism [19]. The regeneration of adventitious shoots is related to the pluripotency of callus tissue cells and their subsequent dedifferentiation and redifferentiation [29]. In the current research, NS inhibited cell reprogramming and stability, possibly by preventing stress-induced epigenetic changes. In mutagenic breeding, despite reduced regeneration capacity, mutation

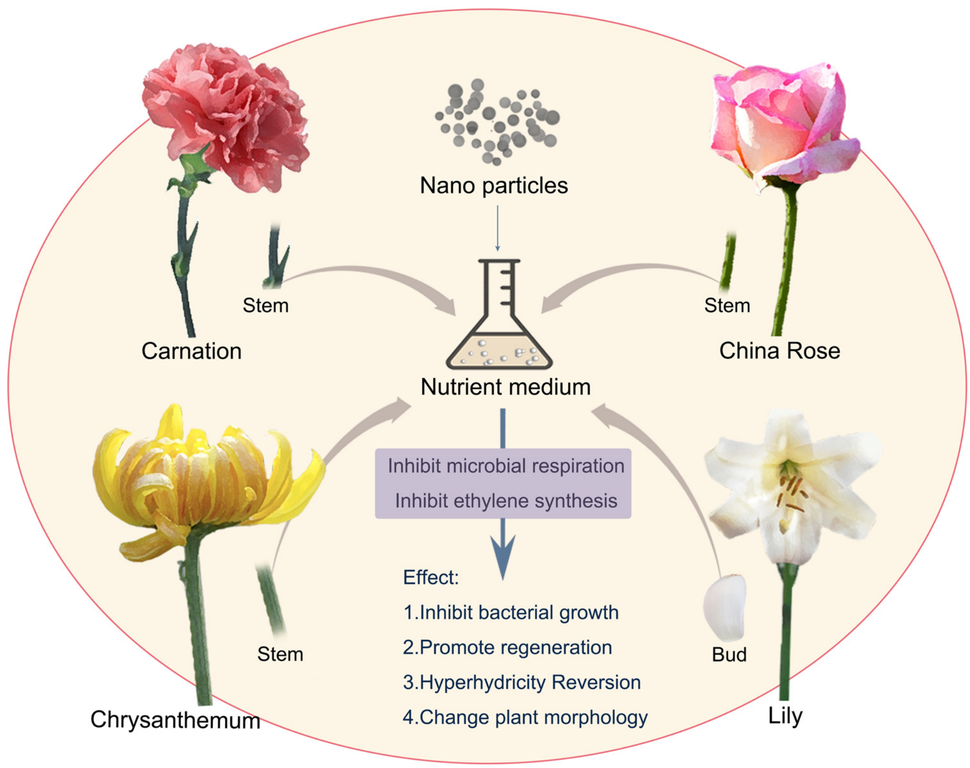

Figure 1: Effects of nanomaterials on different explants of ornamental plants treated with NMs, with NS as an example.

frequencies increased [30]. Therefore, the influence of adding NS to the culture medium is considered an essential source of genetic variation *in vitro* for the propagation of *Chrysanthemum*.

2.2 Application of other metal NMs to ornamental plants

In addition to NS, some other metal NPs have also been reported for their application in the tissue culture of ornamental plants. Zinc (Zn) is an essential micronutrient for plants, serving as a crucial structural regulator for processes such as photosynthesis, auxin synthesis, and cell division [31–33]. This study highlights the exceptional performance of Zn NPs in ornamental plants. Chamani *et al.* found that adding 75 mg/L of ZnO NPs to the culture medium for treating lily bulb scales led to the highest phenolic content in the explants. Additionally, the levels of anthocyanins, chlorophyll, and flavonoids increased, and there was an increase in root length, leaf length, leaf number, and bulb count in the explants [20]. In contrast to previous research, Tymoszuk and Miler applied NS to the explants of *C. morifolium* and *Gerbera jamesonii*, resulting in the inhibition of root regeneration [21]. However, the addition of 10 ppm NG to the culture medium promoted root formation in *G. jamesonii*, with NG exhibiting lower toxicity than NS. Further experiments confirmed that both NS and NG (at 10 ppm) could enhance micropropagation efficiency in *Streptocarpus × hybridus*, while 50 and 100 ppm of NS suppressed the formation of adventitious buds in *Chrysanthemum* [21]. In summary, metal NPs show promise in tissue culture applications for ornamental plants, but the effects of NS application vary among different plant species. It can promote growth in some ornamental plants while inhibiting growth in others.

3 Application of NMs in the growth of ornamental plants

Advancements in nanotechnology have enabled the production of specific NMs with unique properties and wide-ranging practical applications. In recent years, NPs have been recognized as potential biostimulants that can promote plant reproduction and growth [26,34]. Nanofertilizers, as multifunctional and highly efficient fertilizers, can enhance seed vitality, improve plant water and nutrient uptake, boost metabolism, and consequently stimulate root growth in plants.

This not only enhances the resistance of plants to pests, diseases, and various stressors while retaining their original characteristics but also promotes horticultural yield growth, contributing to the sustainable development of horticultural production [4,5]. NS stands out as one of the most intriguing metal NPs, displaying a high level of bioreactivity [35]. Research conducted so far on NS in agricultural and horticultural environments indicates their impact on seed germination, plant growth and development, flowering, yield, and physiological processes [36]. Furthermore, according to current studies, the application of NPs in horticultural plant cultivation can involve various methods, including seed or bulb soaking, foliar spraying, and root irrigation, depending on the plant material type and specific research objectives (Table 2, Figure 2).

3.1 Soaking treatment

Seed soaking is an important step in horticultural plant cultivation. It not only facilitates seed germination and growth but also helps eliminate some pathogenic microorganisms and insect. The application of NS in seed soaking treatment for ornamental plants is also relatively extensive. For example, Parveen and Rao found that treating *Pennisetum alopecuroides* seeds with synthesized NS affected the stem and root growth of the plants, while the slow release of trace amounts of Ag^+ could inhibit harmful fungi and bacteria on the seed surface, thereby increasing seed germination rates [35]. Researchers speculate that this may be due to the dispersed NPs penetrating the seed coat, forming "nano-pores" on the seed coat, thus improving seed germination conditions.

Soaking ornamental plant bulbs with NS also has a positive effect. It was found that soaking bulbs of *Tulipa gesneriana* in 50 and 100 mg/L NS could shorten the production cycle and improve the quality of cut flowers and bulbs [37]. Subsequently, Salachna *et al.* conducted experiments using different concentrations of NS for pre-planting bulb soaking, foliar spray, and substrate soaking with lily. This research demonstrated that pre-planting bulb soaking was the most effective strategy for promoting lily growth and flowering. The study also revealed that NS-soaked bulb or corm treatments promoted plant growth, manifested as an accumulation of leaf and bulb biomass to enhance flowering [38].

NS may also enhance plant growth by improving the accumulation of essential macronutrient absorption in the root system [46]. Bahabadi *et al.* found that the treatment with biologically synthesized NS significantly increased the growth indices and secondary metabolite content of *Cornus officinalis* seeds. Additionally, the increase in proline and phenolic content, along with the upregulation of oxidative stress-related enzymes, suggests the activation of the plant's antioxidant defense mechanisms. Consequently, NS reduces oxidative damage by enhancing the activity of antioxidant enzymes and decreasing the accumulation of reactive oxygen species [39]. This research demonstrates for the first time that NS can serve as an inducer to elicit favorable metabolites and physiological responses, making it a promising strategy in the field of secondary metabolite production for *C. officinalis*.

Currently, research on the physiological effects of NPs on horticultural plants is primarily focused on plant metabolism. Krishnaraj *et al.* conducted an experiment by

Table 2: Application of NMs to promote the germination and growth of ornamental plants

NMs	Species	Application type	Ref.
NS	*P. alopecuroides* (L.) Spreng.	Seed germination and seedling growth	[35]
NS	*Tulipa* × *gesneriana* L.	Preplant bulb soaking	[37]
NS	*L. brownie* var. *viridulum* Baker	Bulb soaking, foliar sprays, and substrate soaking	[38]
NS	*Melissa officinalis* L.	Growth, secondary metabolites, and antioxidant enzymes	[39]
NS	*C. officinalis* Sieb. et Zucc.	Antioxidant enzymes activity	[39]
NS	*Bacop amonnieri* L.	Plant growth metabolism	[40]
NS	*L. albus* L.	Growth potential	[41]
NS	*H. annuus* L.	Foliar spray, morphological characteristics, and carbohydrate content	[42]
Nano NPK	*Gladiolus* × *gandavensis* Van Houtte; *Platycodon grandifloras* (Jacq.) A. DC.	Fertilizer	[43]
Fe_3O_4/HA NMs	*C. morifolium* Ramat.	Photosynthetic pigmentation	[44]
TiO_2 NPs	*Mesembryanthemum cordifolium* L. f.	Solution, root application	[45]
TiO_2 NPs	*A. cordifolia* (L.f.) Schwantes	Seed germination and plant growth	[45]

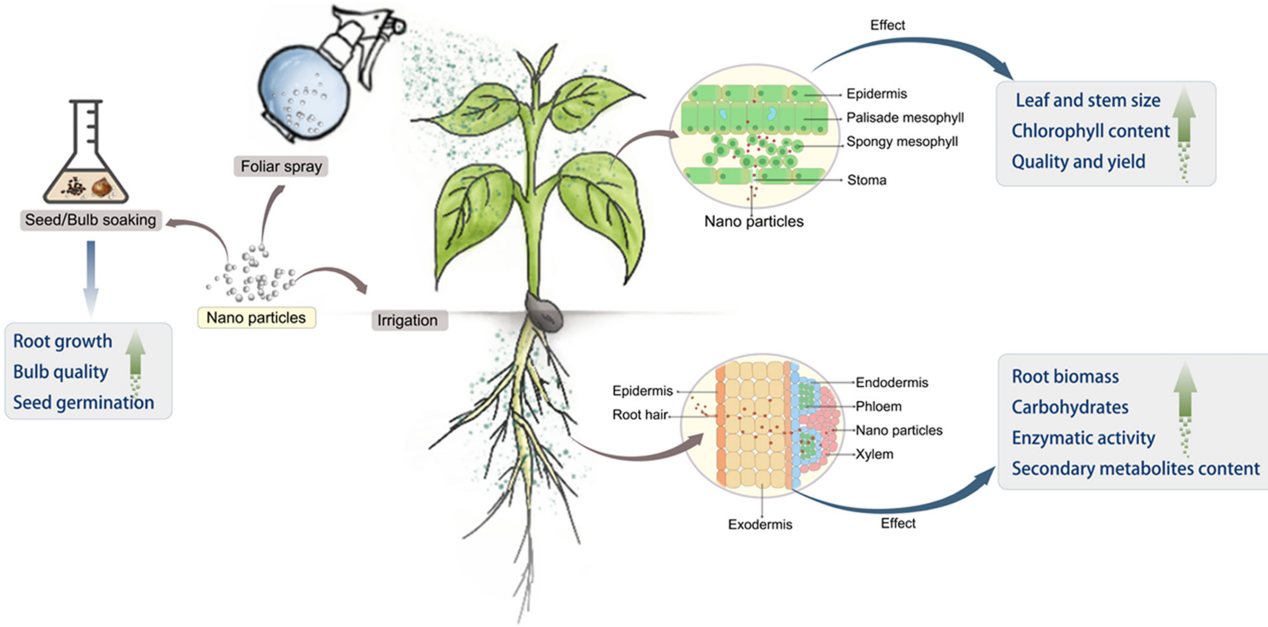

Figure 2: A schematic diagram illustrating the impact of applying NMs to ornamental plants through three methods: seed or bulb soaking, foliar spraying, and root irrigation, respectively.

adding NS and $AgNO_3$ to a hydroponic solution and treating *Bacopa monnieri*. They observed a mild stress response as a result of this treatment. NS significantly reduced the root and stem growth, leading to the disappearance of the root cortex air spaces. This treatment also altered the shape, size, and distribution of elements in the stem's wood region. It resulted in higher levels of proteins and carbohydrates, along with relatively lower levels of total phenolic content, catalase, and peroxidase (POD) enzyme activities [40]. The researchers suggested that this mild stress might be advantageous for enhancing the plant's resistance to pathogen attacks and disease control, but further research is required to understand this mechanism in detail. Al-Huqail exposed *Lupinus albus* seeds to different concentrations of NS and found that at a concentration of 100 ppm NS, the growth was favorable. However, when exposed to higher concentrations of NS (300 and 500 ppm), all growth parameters and indicators significantly decreased [41]. The study suggested that NS may interfere with the activity of certain hydrolytic enzymes required for seed germination, leading to a reduction in germination rate [47]. Morphologically, after treatment with high concentrations of AgNPs, the germinating seeds exhibited poor development of free radicals, and their tips turned brown [48].

Therefore, it is evident that NS also has inhibitory effects on plant growth, so the selection of an appropriate NS concentration is a crucial factor influencing plant growth and development. Due to the incomplete understanding of its mechanisms of action, it is necessary to conduct more in-depth mycological, biochemical, and molecular research to gain a better understanding of NS on plant health and stress response.

3.2 Foliar spraying

In addition to studying the effects of individual NPs on plant growth, exploring the synergistic interactions between NPs and other substances has been gaining prominence. Foliar application of NMs is also a method for promoting the growth of ornamental plants. Yaseen *et al.*, in their research on the effects of foliar application of NS, sodium alginate, and salicylic acid on the growth and nutritional status of sunflowers (*Helianthus annuus*), found that the combined use of 50 mL/L of NS, 1.5 g/L of sodium alginate, and 120 mg/L of salicylic acid had a positive impact on parameters like average leaf number, branch number, and leaf carbohydrate content [42]. As mentioned in Section 2.1, NS is considered to function as an inhibitor of ethylene signal perception [17]. This suggests that the interaction between NS, organic fertilizers, and salicylic acid may promote plant growth by interfering with ethylene biosynthesis. Nevertheless, further research is needed to confirm this.

As it is well known, the content of nitrogen (N), phosphorus (P), and potassium (K) in the soil plays a crucial role in the growth and development of plants. Sarhan *et al.* conducted a study comparing the effects of traditional fertilizers and novel nano-fertilizers on the flowering process and certain chemical components of *Gladiolus grandiflorus*. They found that by foliar spraying with a 10% solution of moringa leaf extract and 1.0 g/L of nano-nitrogen–phosphorus–potassium (nano-NPK), plants exhibited the best flowering and growth results, including increased spike length, flower diameter, and fresh weight. The content of chlorophyll, carotenoids, N, P, K, and total carbohydrates also increased [43]. Therefore, it can be supposed that utilizing the combined effects of NPs with other macro-materials or employing nano-particle composite fertilizers as a novel foliar spraying method can significantly enhance nutrient use efficiency, holding high potential for achieving sustainable agriculture [49,50].

3.3 Root irrigation

In addition to seed soaking and foliar application, NPs can also be absorbed by plant roots through irrigation. Iron is one of the essential elements for plants, playing a crucial role in chlorophyll synthesis and photosynthesis [51]. Iron deficiency, leading to chlorosis in young leaves, is widespread in most calcareous soils in arid and semi-arid regions [51]. Research has shown that iron NPs encapsulated within humic acid (Fe_3O_4/HA NPs) exhibit good biocompatibility and stability, with low toxicity to living cell organisms [52]. Banijamali *et al.* used 20 mg/L of Fe_3O_4/HA NPs to enhance the diversity of photosynthetic pigments in *C. morifolium* “Salvador” and effectively prevented iron chlorosis and iron deficiency [44]. The mechanism of NP action may be related to the influence of its magnetic field on enzyme structures at different stages of enzymatic reactions [53]. The application of the optimal NP concentration could influence the appropriate production of ROS by Fe_3O_4 NPs. Additionally, the positive role of NP encapsulation with humic acid may act as an electron source, increasing the reduction of iron NPs, thus enhancing their biocompatibility and effectiveness in *Chrysanthemum*.

TiO_2 NPs also exhibit photocatalytic properties, and its high surface reactivity can enhance root absorption by generating new vascular elements or increasing water content within the roots [54]. Mohajjel Shoja *et al.* conducted root application of TiO_2 NPs on *Aptenia cordifolia* and revealed a slight reduction in plant growth parameters after treatment, such as plant height, leaf area, dry root weight, and above-ground biomass. However, it showed an increase in chlorophyll, carotenoid, phenolic compounds, and flavonoid content. Microscopic observations also indicated a reduction in vascular bundle diameter and an increase in wall thickness. Furthermore, the study found that *A. cordifolia* could tolerate TiO_2 NPs toxicity up to 20 mg/L, suggesting potential utility in TiO_2 NPs-contaminated regions [45]. Based on this characteristic, phytoremediation, the use of plants to remediate polluted environments, is worth further investigation.

From the above studies, it can be observed that root irrigation with nano-solutions is one effective way to promote plant growth. While NM treatments can enhance plant growth, the unique properties and mechanisms of action of NMs are not yet fully understood. This could potentially pose a threat to the cultivation of ornamental plants. Therefore, it is necessary to conduct more in-depth physiological, biochemical, and molecular research to explore how NMs impact plant health and their mechanisms in responding to stress.

4 NMs can improve stress resistance in ornamental plants

4.1 NMs can improve the resistance of ornamental plants to biotic stress

Ornamental plants are subjected to various types of stresses during their growth, with biotic stresses primarily caused by microbial infections. Currently, the main NMs used in combating bacterial and fungal diseases in ornamental plants are metal oxide NMs and carbon NMs (Table 3).

Hao *et al.* employed three types of carbon NMs, including multi-walled carbon nanotubes (MWCNTs), fullerene (C_{60}),

Table 3: NMs enhance plant resistance to biotic stress

NMs	Species	Application type	Ref.
MWCNTs, C_{60}, rGO, CuO NMs, Fe_2O_3 NMs, TiO_2	*R. rugosa* Thunb.	Gray mold disease agent *B. cinerea*	[55]
MWCNTs, rGO, CuO NMs, TiO_2 NPs	*R. rugosa* Thunb.	*P. pannosa* infection	[56]
Mn_2O_3 NMs, ZnO NMs, CuO NMs	*C. morifolium* Ramat.	Suppresses fusarium wilt, leaf spraying	[57]
TiO_2/Zn NMs	*R. rugosa* Thunb.	Bacterial leaf spot	[58]
NS	*R. rugosa* Thunb.	*B. cinerea* infection	[59]

and reduced graphene oxide (rGO), as well as three types of metal oxide NPs, namely CuO NPs, Fe_2O_3 NPs, and TiO_2 NPs, to treat excised rose petals infected with *Botrytis cinerea*. The results showed that all six NMs had inhibitory effects on gray mold, with the most potent antimicrobial effect observed at a concentration of 50 mg/L for C_{60} and CuO NPs [55].

Subsequently, Hao *et al.* applied four types of NMs, including MWCNTs, rGO, CuO NPs, and TiO_2 NPs by spraying detached rose leaves. They found that at a concentration of 200 mg/L, all four NMs were capable of inhibiting the infection of *Podosphaera pannosa*, with CuO NPs exhibiting the strongest antifungal activity. Furthermore, the treatment increased the levels of the endogenous hormones zeatin riboside (ZR) and dihydrozeatin riboside (DHZR) in plants, enhancing their resistance to fungal infection [56]. ZR and DHZR are two major endogenous cytokinins in plant leaves that can delay leaf senescence, accelerate cell division, and improve stress resistance [60]. The increase in ZR levels in infected leaves after CuO NPs treatment suggests that CuO NPs can act as an exogenous hormone inducer, enhancing the rose's resistance to *P. pannosa*.

Elmer *et al.* conducted experiments on *C. morifolium* using different metal oxide NMs including Mn_2O_3 NPs, ZnO NPs, and CuO NPs. They found that plants treated with CuO NPs not only significantly reduced the infection of *Fusarium oxysporum* f. sp. Chrysanthemi, but also improved the horticultural quality of the plants. In contrast, the antibacterial effect of Mn_2O_3 NPs was less stable, and the treatment with ZnO NPs had almost no impact [57]. This suggests that CuO NPs have a unique efficacy in enhancing plant health and quality. However, whether CuO NPs induce changes in related hormone levels to enhance resistance is not further discussed in this study. In the medicinal plant *Cassia quadrangularis*, CuO NPs inhibited the growth of *Aspergillus niger* and *Aspergillus flavus*, mainly by disrupting the cytoplasm and accelerating their apoptosis rate [61]. While the specific mechanisms of action of metal oxide NMs in ornamental plants have not yet been discovered. Furthermore, a green-synthesized NM, SeNP, has been shown to enhance the resistance of wheat against spot blotch disease, but its role in the defense against fungal diseases in ornamental plants has not been studied [62].

Compared to research on fungi, there is relatively less research on the use of NMs in combating bacterial infections in ornamental plants. Paret *et al.* studied the impact of TiO_2/Zn NP on the resistance of *Rosa rugosa* to bacterial leaf spot and found that TiO_2/Zn NP reduced the *in vitro* cell viability of *Xanthomonas* sp. Additionally, TiO_2 NPs possess photocatalytic properties, generating highly chemically active hydroxyl and superoxide radicals in the presence of light, thereby exhibiting antimicrobial effects. Field application of TiO_2 NPs on plant leaves can induce photocatalysis, leading to the death of bacteria cells and significantly reducing the severity of the disease spots [58].

In summary, in ornamental plants, NMs have a dual role. On the one hand, due to their smaller size than the cell wall pores, NMs may enter the air spaces within plant cells and be absorbed by plants in various forms, including polymers, carbon, metals, and metal oxides, and they are transported to other parts of the plant through transport tissues, affecting the plant [63]. On the other hand, they can also act as inducers of plant hormones, stimulating an increase in hormone expression within the plant, thereby enhancing the plant's disease resistance [28].

4.2 NMs can improve the tolerance of ornamental plants to abiotic stress

Ornamental plants may also encounter abiotic stresses during growth, including salt stress, drought stress, water stress, high-temperature stress, and heavy metal stress, while reducing plant yield and, in severe cases, even leading to plant death. Among these stresses, salt stress can disrupt the osmotic balance system, inhibit nutrient absorption in plants, and severely impact plant growth [64]. Some NMs have been proven to have potential in enhancing the tolerance of ornamental plants to salt stress (Table 4). Asgari and Diyanat found that using nano-silica or potassium silicate fertilizers reduced the negative impact of salt stress on miniature rose plants, improving their growth status. Further research revealed that silicon application reduced the concentrations of K, P, iron, and Zn in rose buds [65]. Additionally, Byczyńska discovered that treating lily bulbs with colloidal NG not only enhanced salt tolerance in plants but also increased bulb fresh weight and diameter, ultimately improving lily bulb yield [66].

Drought stress significantly affects various life processes of plants, including their growth, development, and reproduction, making it one of the extensively researched environmental stress factors. The application of NMs can alleviate drought stress in ornamental plants to some extent. Azad *et al.* conducted a study on seven different genotypes of *Chrysanthemum lavandulifolium* under drought stress conditions. They observed that foliar application of nanocomposites with iron led to increased antioxidant enzyme activity and flower yield. Interestingly, the effects varied among different genotypes, showing both positive and negative responses [69]. Zhao *et al.* found that GO mitigates damage from drought stress in three kinds of peonies by enhancing plant growth, antioxidant enzyme activity, and

Table 4: Effects of NMs on abiotic stress

NMs	Species	Application type	Ref.
Nano-silicon	*Rosa chinensis* var. *minima* (Sims) Voss	Salt stress	[65]
Nano-colloidal silver	*L. brownii* var. *viridulum* Baker	NaCl stress	[66]
GO	*P. ostii* T. Hong & J.X. Zhang	Soil water retention agent	[67]
Nano-iron chelated	*C. lavandulifolium* (Fisch. ex Trautv.) Makino	Drought stress	[68]
MWCNTs	*Brassica napus* L. *H. annuus* L. *Cannabis sativa* L.	Cadmium stress	[68]
MWCNTs	*P. ostii* T. Hong & J.X. Zhang	Drought stress	[69]
MWCNTs	*T. erecta* L.	Pb and Cd stress	[70]
TiO_2 NPs	*C. roseus* (L.) G. Don	Water stress	[71]

photosynthesis. Additionally, due to the soil environment and electrostatic repulsion between GO and the plant roots, GO does not accumulate in the plant, thus causing no toxicity. Furthermore, the presence of hydrophilic oxygen-containing functional groups in GO helps prevent soil moisture evaporation without altering soil pH, making it an effective soil water retention agent [72].

Zomorrodi *et al.* found that under conditions of water deficit, the ornamental quality of *Catharanthus roseus*, such as stem strength and longevity, significantly deteriorated. Furthermore, the plants exhibited reduced chlorophyll content, increased membrane degradation, and oxidative damage such as lipid peroxidation. Spraying TiO_2 NPs (0.5 mM being the most effective) effectively alleviated the water deficit in the plants. This not only improved ornamental quality but also increased carotenoid content, as well as the activities of hydrogen peroxide and POD enzymes. This approach provides a practical method to enhance the ornamental characteristics of *C. roseus* and extend its ornamental lifespan [71]. Overall, NMs reduce oxidative stress and combat environmental stressors such as drought by enhancing the activity of plant antioxidant enzymes (Figure 3).

In the realm of ornamental plants, there have been studies on how to utilize NMs to mitigate the impact of high-temperature stress on plants, including peonies. Zhao *et al.* found that MWCNTs have potential preventive effects in reducing damage induced by high temperatures in *Paeonia ostii*, with 200 mg/L as the most effective treatment concentration. MWCNTs can activate the ascorbate–glutathione cycle, thereby enhancing its antioxidative capacity and photosynthesis to combat high-temperature stress [67].

Soil contaminated with heavy metals can also exert adverse effects on the growth and development of plants and microorganisms, leading to decreased crop productivity. Due to the substantial surface area and strong catalytic and adsorption capabilities inherent to NPs, they have a certain potential for remediating heavy metal-contaminated water bodies and soils. Oloumi *et al.* found that MWCNTs could effectively alleviate the growth inhibition

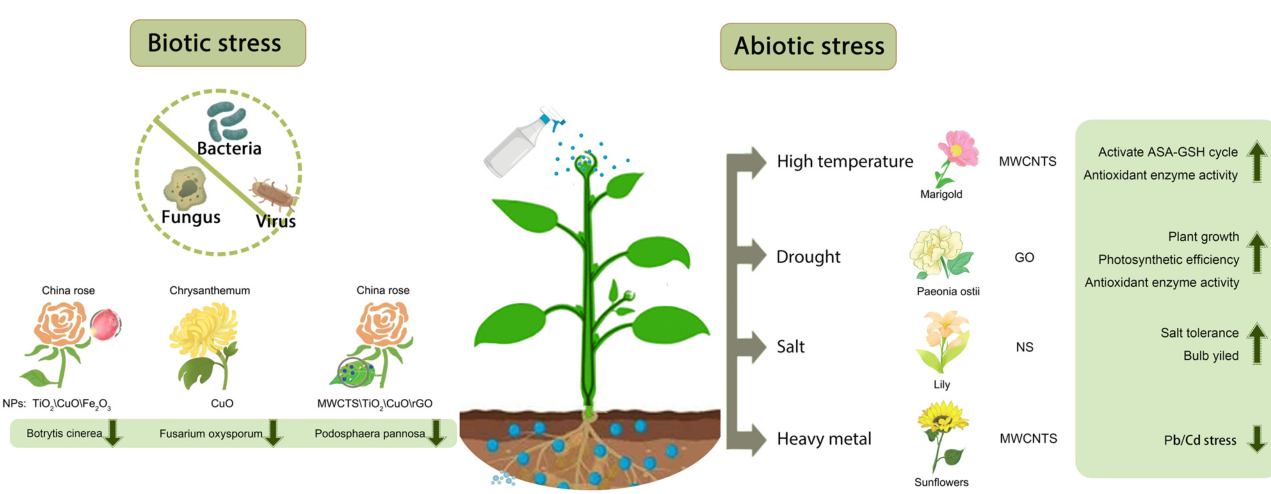

Figure 3: Schematic diagram of the mechanism by which NMs enhance the resistance of ornamental plants to biotic and abiotic stresses.

of *H. annuus* seedling roots and stems induced by Pb or Cd stress. Furthermore, they contributed to increased chlorophyll content. It is worth noting that seedling growth parameters and the accumulation levels of heavy metals in plants were significantly associated with the concentration of MWCNTs and the plant species [68]. Similarly, Sharifi *et al.* found that applying 250 mg/L of MWCNTs to the leaves could enhance the antioxidant enzyme activity of *Tagetes erecta* and reduce oxidative damage under Pb and Cd stress. This promoted plant growth and recovery. However, high concentrations of MWCNTs were toxic to the plants [70].

NM-plant co-remediation is considered an effective approach to overcome the bottleneck in heavy metal remediation. However, it is crucial to pay attention to the application concentration during the process. In summary, NMs play a dual role in assisting ornamental plants in coping with abiotic stressors. First, their high adsorption capacity and ease of absorption due to their structural properties. Second, they enhance the plant's antioxidant capabilities at a metabolic level, thereby mitigating oxidative damage to the plants.

5 Roles of NMs in postharvest physiology of ornamental plants

The post-harvest quality of cut flowers determines their trade on the international market and consumer acceptance. Carefully cultivated fresh flowers are highly sensitive to oxidative damage during post-harvest maintenance and transportation. To ensure the quality of cut flowers, a significant amount of chemicals is consumed in the floral industry for preservation. Therefore, the development of technologies that enhance the quality and shelf life of fresh flowers is crucial, and nanotechnology is one of the most important methods for reducing chemical usage and improving input efficiency. It has been reported that NS particles release Ag^+ that interact with cytoplasmic components, disrupting membrane permeability and significantly acting as an ethylene inhibitor [73]. Furthermore, NS reduces water uptake through aquaporins, making it a commonly used solution to extend the vase life of cut flowers [74].

5.1 NS is a common preservative for cut flowers

The reasons for the aging of cut flowers vary, and one of the main factors contributing to the short post-harvest lifespan and poor quality of ethylene-insensitive cut flowers is microbial growth in the vase solution, which can lead to blockages in the xylem vessels, hindering water uptake [75]. For some ethylene-sensitive cut flowers, their post-harvest lifespan is closely related to the transcription levels of genes involved in ethylene biosynthesis [76]. For ethylene-insensitive cut flowers, it is common to use antimicrobial agents in the vase solution to control microbial growth. However, these agents may have some impact on the quality and physiology of cut flowers. Studies suggest that NS can inhibit microbial growth while maintaining cut flower quality. NS treatment not only extends the vase life of cut flowers like Oriental lily, rose, *G. jamesonii*, and carnations (*Dianthus caryophyllus*), but also improves their visual characteristics, promotes water absorption, and effectively inhibits microbial proliferation [71,75,77–81].

Furthermore, some studies have validated the positive effects of NS through microscopic or visual examinations. For example, Li *et al.* observed that NS effectively suppressed bacterial colonization and biofilm formation in stem-end cut surfaces and woody vessels using confocal laser scanning microscopy and scanning electron microscopy [82]. Amin found that NS treatment improved the visual features of anthurium (*Anthurium andraeanum* Londen) spathe, such as color and appearance [83]. Several studies have also explored the effects of mixing NS with other substances in cut flowers. For instance, Geshnizjany *et al.* combined post-harvest calcium chloride spraying and NS addition to the vase solution for *G. jamesonii*, inhibiting microbial growth at the stem tips and extending the cut flowers' lifespan [84]. Researchers have also found that the most effective approach is the combined application of NS with plant growth regulators like gibberellins (GAs) for carnations cut flowers [85]. Sun *et al.* studied the combined use of NS and 8-hydroxyquinoline (8-HQ) and discovered that it significantly prolonged the vase life of peonies compared to the control group. It also slowed down the decline in protective enzyme activity during late storage [86]. In summary, NS treatment effectively alleviates microbial-induced xylem blockages, enhances water uptake by cut flowers, maintains their relative fresh weight, and provides superior results compared to some common ethylene inhibitors.

For ethylene-sensitive cut flowers, methods involving the inhibition of ethylene biosynthesis can be applied. This includes the use of ACC synthase inhibitors such as amino-oxyacetic acid and aminoethoxyvinylglycine, or ACC oxidase inhibitors like salicylic acid to restrain ethylene biosynthesis and prevent bacterial growth. Kim *et al.* first introduced the idea that NS can be employed to inhibit ethylene production in cut lily "Sibera" [87]. Since then, an increasing number of researchers have been using NS to control ethylene in pulse treatments and vase solutions, thereby extending the lifespan of cut flowers like roses, lisianthus (*Eustoma grandiflorum*), carnations, *G. jamesonii*, among others. This approach inhibits bacterial proliferation at the stem end, counteracts ethylene, and thus delays the senescence of cut flowers [77,88–90].

Furthermore, a study by Skutnik *et al.* found that NS treatment with the addition of sucrose is more effective in extending the vase life of lisianthus in comparison to the application of the ethylene inhibitor 8-HQC. NS treatment not only increased stem uptake strength and transpiration rate but also significantly reduced the activity of hydrogen POD in both the upper and lower stem sections of the flowers, enhancing the overall condition of cut flowers [91]. Consequently, it is evident that NS treatment effectively mitigates bacterial-induced blockages in the xylem, enhances water uptake in cut flowers, and maintains their relative fresh weight, with superior results when compared to some common ethylene inhibitors.

5.2 Study on the mechanism by which NS affects cut flowers at the molecular level

In the last few years, researchers have been delving into the molecular-level effects of NS treatment on cut flowers. Specifically, Naing *et al.* conducted an extensive study on how NS treatment can delay the aging process of carnation petals. They analyzed the gene expression levels of petals and pistils from initial bloom to aging and found that NS may work by inhibiting the expression of petal aging-related genes (CPI) and ethylene biosynthesis genes (ACS and ACO). This active regulation of ethylene signaling genes in petals and pistils was accompanied by increased activity of antioxidant enzymes and cysteine proteases, significantly suppressing ethylene production and consequently delaying petal aging [92,93].

Zhao *et al.* revealed that NS treatment significantly extended the vase life of *P. ostii* cut flowers while also inhibiting the growth of microorganisms at the stem base, increasing relative water uptake, and distributing silver ions. Furthermore, they discovered that three aquaporin genes, including two plasma membrane intrinsic protein genes PlPIP1;2, PlPIP2;1 and one nodulin-like intrinsic protein gene PlNIP, collectively played a role in maintaining cut flower water balance and effectively preserving fresh weight and flower diameter [94]. Ha and In used NS treatment on both ethylene-sensitive rose "Matador" and ethylene-insensitive rose "Dolcetto" cut flowers. They found that NS treatment significantly inhibited the increase of ethylene biosynthesis genes induced by ethylene and decreased the ethylene receptor gene expression in petals. This led to reduced ethylene responsiveness in both types of roses, significantly improving their postharvest quality and vase life. NS treatment also suppressed bacterial growth at the stem base by enhancing solution uptake [59]. These research findings indicate that NS effectively prolong the vase life of cut flowers by reducing ethylene production and minimizing water stress. However, choosing the appropriate concentration is crucial for specific plant genotypes to avoid potential phytotoxic effects, as plant toxicity could adversely affect cut flower longevity.

5.3 Applications of other NMs to cut flowers

Apart from the application of NS in cut flowers, there has been research using some other NMs in recent years. For instance, He *et al.* treated rose cut flowers with 0.1 mg/L GO, and Thakur *et al.* used both GO and NS to treat *Strelitzia reginae*, which not only effectively inhibited the growth of microorganisms at the stem ends but also increased stem section water uptake rate and moisture balance, thereby extending the cut flower's lifespan [36,95]. García-González *et al.* found that CaO NPs could strengthen the stems of *G. jamesonii*, reduce stem bending and weight loss, maintain the visual quality, and increase chlorophyll content. This also enhanced its antioxidant capability without affecting the synthesis of phenolic compounds. Therefore, CaO NPs can be considered an effective vase solution for post-harvest preservation of *G. jamesonii* [96]. Sánchez-Navarro *et al.* used SiO_2 NPs in the production of lilies, which increased mineral content and leaf surface chlorophyll content while enhancing its antioxidant capacity. This significantly improved the flower quality and shelf life of the lilies [97].

Carbon NMs possess outstanding chemical, physical, electrical, structural properties, and good biocompatibility [98]. Zhang *et al.* studied the protective effects of three types of single-walled carbon nanotubes, graphene GQD, and C_{60} on the antioxidant activity and aging of plant cells using *D. caryophyllus* cut flowers as a model. They found that appropriate concentrations of C_{60} and GQD could affect reactive oxygen metabolism and downstream biological events, including cellular redox status, the antioxidant system, membrane lipid peroxidation, and so on, effectively delaying the aging and senescence of plant tissues [99]. Li *et al.* found that in cut chrysanthemum "Jinba," the combined treatment of 5 mg L^{-1} MWCNTs, with 30 g L^{-1} sucrose, and 0.2 g L^{-1} 8-HQ could effectively promote the water and sugar uptake in flowers, thus accelerating bud opening, maintaining larger inflorescence diameter, and extending the vase life [100].

In summary, NMs with antibacterial properties, when used as effective preservative solutions, can extend the vase life of cut flowers. Commonly used antibacterial NMs not only inhibit the growth of microorganisms by increasing the membrane permeability of vase solutions but also inhibit the biosynthesis of ethylene and enhance the activity of antioxidant enzymes (Figure 4).

6 Conclusion and outlook

Based on these research studies, NMs can essentially be applied to most stages of horticultural plant growth, development, and production, including tissue culture, seed vitality and germination, seedling growth, material transport, post-harvesting, and yield, showing significant development potential [101]. In this article, we provide a relatively comprehensive overview of the application of NMs in ornamental plants. During the process of plant tissue culture, an appropriate concentration of metal NPs, especially NS, plays a positive role in inhibiting microbial growth and mitigating excessive moisture levels in plants. Moreover, it can have certain impacts on the growth and development of plants. However, current research has mainly focused on popular ornamental plants such as *Chrysanthemum*, lilies, and roses, with limited knowledge about the functions in most ornamental plants. The effects of different types of NMs on various ornamental plants vary because different cultivation varieties exhibit differences in biochemical responses, *in vitro* regeneration efficiency, genetic variations, and induction mutation frequencies [102]. Additionally, NMs offer outstanding biocompatibility, the ability to safeguard exogenous nucleic acids from damage, and efficient transfection capabilities, providing a novel avenue for plant genetic transformation technology. While significant breakthroughs have been achieved in this field in model plants like *Arabidopsis* and tobacco and in major crops such as rice, corn, and wheat [103,104], it remains relatively unexplored in the realm of ornamental plants. The development of genetic engineering technology in ornamental plants lags behind that of fruits, vegetables, and other plants. Therefore, the use of NMs for genetic transformation of receptor cells in ornamental plants holds extensive application potential.

From the cultivation perspective, NMs, when applied through methods such as seed soaking, foliar spraying, and root application, have promoted the root growth of ornamental plants, enhanced water and nutrient absorption, increased enzyme activity, and improved the plant's resistance to biotic and abiotic stresses. Some NMs also serve as biostimulants, enhancing plant health and inducing plant defense mechanisms. However, the mechanisms for NMs uptake by plant cells are closely related to the physical and chemical properties of the materials, including size, shape, composition, surface charge, and the transport processes in the apoplastic and symplastic pathway, which require further investigation. While the application of NMs has shown positive effects on horticultural crops, helping to alleviate various environmental stresses, it is important

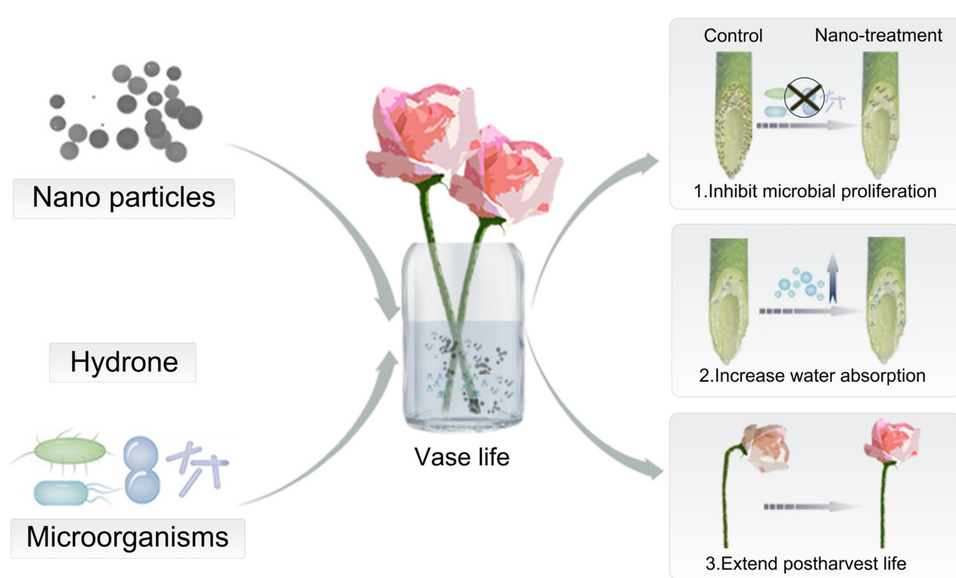

Figure 4: Mechanism of NMs extending the lifespan of cut flowers.

to note that different plant species may require different types of NMs, and not all NMs possess the appropriate defense capabilities [105]. Moreover, nanotoxicity remains a bottleneck for the unrestricted use of NMs in biological systems. Therefore, before applying NMs, a thorough investigation of the material's relevant physicochemical properties, including size, shape, composition, surface area, application method, redox state, and dosage, should be conducted to mitigate ecological and toxicological risks to both plants and humans [10]. Given these challenges, more rigorous research is needed to gain a deeper understanding of the physiological, biochemical, and molecular mechanisms of NM effects on plants.

In this review, it becomes evident that NMs exhibit excellent antimicrobial properties in ornamental plants, whether in tissue culture, post-harvest management of cut flowers, or in combating biotic stress during the growth process. While it is generally believed that the induction of oxidative stress by NMs in plant systems, through the generation of ROS, is the underlying cause of various effects, further research is needed to confirm this hypothesis. Despite the majority of literature establishing the substantial potential of NMs in aiding ornamental plants in resisting both biotic and abiotic stresses, most research results merely present surface-level phenomena. Comparative to other commonly used biochemical materials, we still require deeper exploration of the physiological, biochemical, and molecular mechanisms of NM-mediated plant health processes. Additionally, as a crucial tool for promoting normal plant growth and development, one of the future's key development directions is to create low-cost, versatile, and environmentally friendly NMs.

Undoubtedly, with the ongoing development of nanotechnology, our understanding, synthesis, and application of NMs continue to evolve. In the realm of ornamental plants, the applications of NMs encompass but are not limited to callus induction, plant growth promotion, resistance against biological and abiotic stresses, post-harvest management, regulation of plant gene expression, and interactions with biomolecules, gradually diversifying the field. To address long-standing critical issues in ornamental plant growth and industry, interdisciplinary collaboration is indispensable, with nanotechnology playing an essential role therein. In summary, we firmly believe that nanotechnology will have far-reaching impacts on the growth, production, and sustainable development of ornamental plants. We also hope that this review article can assist researchers in both the fields of plant science and nanoscience in making informed choices regarding NMs suitable for various ornamental plants, thereby fostering the widespread adoption of new technologies.

Funding information: This work was supported by the National Natural Science Foundation of China (32071812), Beijing Academy of Agriculture and Forestry Sciences Specific Projects for Building Technology Innovation Capacity (KJCX20230108), and Programs for Science and Technology Development of Henan province (232102110236; 242102110316).

Author contributions: All authors have accepted responsibility for the entire content of this manuscript and approved its submission.

Conflict of interest: The authors state no conflict of interest.

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