



Paradoxical effects of nanomaterials on plants: Phytohormonal perspective exposes hidden risks amidst potential benefits

Parammal Faseela^a, Joy M. Joel^b, Riya Johnson^b, Edappayil Janeeshma^c, Puthukkollu P. Sameena^d, Akhila Sen^e, Jos T. Puthur^{b,*}

^a Department of Botany, Korambayil Ahamed Haji Memorial Unity Women's College, Manjeri, Malappuram, Kerala, 676122, India

^b Plant Physiology and Biochemistry Division, Department of Botany, University of Calicut, C. U. Campus P.O., Malappuram, Kerala, 673635, India

^c Department of Botany, MES KEVEEYAM College, Valanchery, Malappuram, Kerala, 676552, India

^d Department of Botany, PSMO College, Tirurangadi, Malappuram, Kerala, 676306, India

^e Department of Botany, Mar Athanasius College, Kothamangalam, Ernakulam, Kerala, 686666, India

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ABSTRACT

The rapid growth of nanotechnology has led to the production of a significant amount of engineered nanomaterials (NMs), raising concerns about their impact on various domains. This study investigates the negative interactions between NMs and phytohormones in plants, revealing the changes in signaling crosstalk, integrated responses and ecological repercussions caused by NM pollution. Phytohormones, which include auxins, cytokinins, gibberellins, abscisic acid, ethylene, jasmonic acid, salicylic acid and brassinosteroids are essential for plant growth, development, and stress responses. This review examines the intricate relationships between NMs and phytohormones, highlighting disruptions in signaling crosstalk, integrated responses, and ecological consequences in plants due to NM pollution. Various studies demonstrate that exposure to NMs can lead to alterations in gene expression, enzyme functions, and ultimately affect plant growth and stress tolerance. Exposure to NMs has the capacity to affect plant phytohormone reactions by changing their levels, biosynthesis, and signaling mechanisms, indicating a complex interrelation between NMs and phytohormone pathways. The complexity of the relationships between NMs and phytohormones necessitates further research, utilizing modern molecular techniques, to unravel the intricate molecular mechanisms and develop strategies to mitigate the ecological consequences of NM pollution. This review provides valuable insights for researchers and environmentalists concerned about the disruptive effects of NMs on regulating phytohormone networks in plants.

Abbreviations

ABA	abscisic acid
ABF	ABA RESPONSIVE ELEMENT-BINDING FACTOR
ACO	1-Aminocyclopropane-1-Carboxylic Acid Oxidase
ACS2	aminocyclopropane-1-carboxylic acid synthase 2
Ag NM	Silver Nanomaterial
Ag ₂ S NM	silver sulphide nanomaterials
Al ₂ O ₃	aluminium oxide
ARF	Auxin Response Factors
ARR	<i>Arabidopsis</i> Response Regulators
Aux/IAAs	Auxin/Indole-3 Acetic Acid
BAK1	brassinosteroid insensitive 1-associated receptor ki-

nase 1

BES1	BRI1-EMS-suppressor 1
BR	brassinosteroids
BZR1	brassinazole-resistant 1
CAT	catalase
CBP60	cam-binding protein 60-like G
CeO ₂ NM	Cerium Oxide Nanomaterial
CK	cytokinins
CNTs	carbon nanotubes
CPS	Ent-copalyl diphosphate synthase
CTR1	Constitutive Triple Response 1
CuO NM	Copper Oxide nanomaterials
EIN1	ethylene-insensitive 1

* Corresponding author.

E-mail address: jtputhur@yahoo.com (J.T. Puthur).

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<i>EIN2</i>	<i>ethylene insensitive 2</i>
<i>EIN3</i>	<i>ethylene insensitive 3</i>
<i>ERS1</i>	<i>Ethylene Response Sensor 1</i>
ET	ethylene
ETR1	Ethylene Response/Receptor 1
Fe ₂ O ₃ NM	Iron Oxide Nanomaterial
GA	gibberellins
GID1	Gibberellin Insensitive Dwarf1
IAA	Indole-3-Acetic Acid
<i>ICS</i>	<i>isochorismate synthase 1</i>
<i>IPT</i>	<i>Isopentenyl transferase</i>
JA	jasmonic acid
<i>KS</i>	<i>Ent-kaurene synthase</i>
La ₂ O ₃ NM	Lanthanum Oxide Nanomaterial
<i>Momordica charantia</i>	<i>M. charantia</i>
MWCNTs	Multiwalled CNTs
<i>NCED3</i>	<i>Nine-cis-epoxycarotenoid dioxygenase 3</i>
NMs	nanomaterials
POX	peroxidase
PS NMs	polystyrene NMs
<i>RD22</i>	<i>Dehydration-responsive gene</i>
<i>RGA1</i>	<i>Repressor of Gibberellic Acid 1</i>
ROS	Reactive Oxygen Species
SA	salicylic acid
SiO ₂	silicon dioxide
SOD	superoxide dismutase
TiO ₂	titanium oxide
ZnO NM	Zinc Oxide Nanomaterial
ZnO	zinc oxide.

1. Introduction

Due to the rapid growth of nanotechnology, the domains of biological, commercial, ecological, and computational modelling have all seen significant changes in the last 10 years. Engineered Nanomaterials (NMs) are synthesized through various processes which have unique and extraordinary features that are never found among their respective bulk. As a result, tons of these nanosized materials are generated annually in the industrial sector in large amounts. When discharged into the environment, NMs may interact with pre-existing pollutants, resulting in a cascade of biological events (Deng et al., 2017). An extensive review by Ka et al. (2018) have clearly thrown light on the destiny, movement, and transformation of NMs released into the environment, which can possibly impact the environment in an adverse manner.

A number of entry points, including stomata, root hairs, and surface fractures on leaves, allow NMs to enter the plant system. After entering, they may spread by bulk flow, phloem loading, or by diffusion to reach their appropriate targets (Khan et al., 2022b). Several scientific studies have revealed that NMs can induce various harmful physiological and cellular impacts on plants. These effects include interference with chlorophyll synthesis, chromosomal abnormalities, changes in transpiration rate, diminished seed germination, inhibition of root growth, harm to cell membranes, disturbance of redox homeostasis, delayed development, and a decrease in biomass (Chung et al., 2019; Azhar et al., 2023; Thiruvengadam et al., 2024).

Phytohormones are chemical messengers produced by plants in very low quantities, possessing the capacity to regulate diverse growth and developmental processes of the plant (Jiang and Asami, 2018). In reaction to various biotic and abiotic stresses, these substances can trigger distinct signal transduction pathways (Rhaman et al., 2021). In order to recognize and define various molecular pathways involved in phytohormones-mediated stress response in plants, many research techniques,

including expression profiling, bioinformatics, proteomics, mutant screening, microarray, etc. have been investigated (Saini et al., 2021). When plants are exposed to stresses, they synthesize and accumulate defense-related phytohormones such as ethylene (ET), abscisic acid (ABA), gibberellins (GA), brassinosteroids (BR), salicylic acid (SA) and jasmonic acid (JA) more readily than growth-promoting phytohormones such as auxins and cytokinins (CK) (Montero-Palmero et al., 2014). As a result, plants would be able to withstand unfavourable conditions and would experience an acceleration to their stress responses. Furthermore, this would ensure that the plant is capable of growth revival when environmental constrain is decreased (Sabagh et al., 2022).

The developmental process and growth responses of plants depend on the signaling cascades regulated by various growth phytohormones (Schepetilnikov and Ryabova, 2017). Major plant hormones include auxins, CK, GA, ABA, ET, JA, SA and BRs. Crosstalk among the various phytohormones is found to be antagonistic or synergistic. In addition, components of signaling pathway of one plant hormone interact with the signaling components of other hormones. The crucial role of signaling cascades regulated by phytohormones in plant growth and stress tolerance have been explored. TIR1/AFBs, Aux/IAAs, and auxin response factors (ARFs) are the major components involved in auxin signaling pathway. Under auxin rich environment, auxin bind to TIR1/AFBs, as a result Aux/IAAs are marked for degradation (Caumon and Vernoux, 2023). The degradation of Aux/IAA aid to initiate the expression of ARF gene, and the ARF factors synthesized activate or repress a series of genes regulating the functions of plants (Morffy and Strader, 2022). ARFs are transcription factors with conserved DNA binding domain and different analysis have unraveled the role of ARF in leaf senescence, floral organ development, embryonic root formation, vasculature, pollination, fertilization and control of sugar metabolism (Li et al., 2016). CKs help in the functioning of normal development and stress responses in plants (Li et al., 2022a). A two-component signaling system is regulating the activities of CKs. Sensor kinases, histidine phosphotransfer proteins, and response regulators are the major elements of CK signaling cascade. The cytokinin sensor kinases are activated under the presence of CK by autophosphorylation. The phosphate group transferred in this process is then transferred to a histidine phosphotransfer protein which activates specific response regulators. These response regulators influence the up-regulation or down-regulation of the signaling mechanism that affect gene expression of plant cells (Powell and Heyl, 2023).

ABA is regulating almost 10% of plant gene expression (Li et al., 2022b). In the presence of ABA, *PYRABACTIN RESISTANCE 1* (*PYR1*) inhibits the action of the phosphatase *ABI1-INSENSITIVE1* (*ABI1*). This leads to the activation of SNF1-related protein kinases (subfamily 2) (*SnRK2s*). These molecules activate several transcription factors from the *ABA RESPONSIVE ELEMENT-BINDING FACTOR* (*ABF*) family. Activation of ABFs cause significant changes in the expression of a large number of plant genes (Du et al., 2022). The hormone GA is influenced by critical negative regulators such as DELLA proteins (Zhang et al., 2023). In the presence of GA, GID1 triggers the degradation of DELLAs and releases transcription factors (TFs) and prefoldins (PFDs). Further GA activate *PHYTOCHROME INTERACTING FACTORS* (*PIFs*) that negatively regulate light signaling and promotes growth in terms of elongation (Chai et al., 2022). Another major hormone, ET suppresses the activity of its receptors, found in cell membrane of the endoplasmic reticulum (Zhou et al., 2022). Ethylene response/receptor 1 (ETR1), ethylene response sensor 1 (ERS1) are the major receptors group found in ET signaling (Wang et al., 2022).

A multitude of scientific investigations have brought to light the capacity of NMs to instigate a wide array of positive physiological and cellular impacts on plants (Al-Khayri et al., 2023; Ijaz et al., 2023). These studies have demonstrated that NMs can facilitate improvements in plant growth, nutrient absorption, and stress response mechanisms. Additionally, they have revealed the potential of NMs to enhance photo-

synthetic efficiency, increase crop yield, and confer resistance to environmental stressors. NMs provide better resistance to plants against drought stress by improving photosynthetic efficiency, accumulating various osmolytes, hormones, phenolics and enhancing antioxidant enzyme activities and gene expression (Rasheed et al., 2022). Moreover, Tripathi et al. (2022) investigated the effect of NMs to ameliorate the biotic and abiotic stress consequences in plants with the regulation of phytohormones signaling for improvement in stress tolerance of plants. Such findings hold promise for the development of innovative NM-based strategies aimed at enhancing plant productivity and resilience in agricultural and ecological settings.

Lately, there has been a growing inclination to widely employ engineered NMs in agricultural sector owing to their advantages. However, it's essential to recognize and understand the influence of NMs on plants may not always be advantageous. Recent studies, have explored the ecological impacts of (silver sulphide, Ag₂S) Ag₂S NM. The findings revealed that plants like cucumber (*Cucumis sativus*) and wheat (*Triticum aestivum* L.), have the potential to absorb nanosilver from the soil (Wang et al., 2017). The uptake of NM resulted in the activation of genes related to the ethylene (ET) signaling pathways, leading to a decline in plant growth. Additionally, NMs exhibit adverse effects on the expression of the exogenous *Bt* gene in Bt-transgenic cotton, potentially enhancing insect resistance but also impacting phytohormone concentrations (Le Van et al., 2014, 2016). Previous transcriptomic studies have indicated transcriptional changes in the biosynthesis or signal transduction of plant hormone genes, involving downregulation of auxin response genes, ABA biosynthetic genes, ethylene (ET) signaling components as well as the downregulation of genes involved in pathogen response (Syu et al., 2014). This review provides an overview of our knowledge on the interactions between NM and plants, which can cause disruptions in phytohormone signaling and to pinpoint potential areas for further research that can address current knowledge gaps in the literature.

2. Nanotechnology: types and properties

NMs with a dimension sized between 1 and 100 nm (10⁻⁹ m), differ from their bulk counterparts in terms of their physical and chemical properties due to the increased surface area/volume ratio caused by the decrease in size (Roduner, 2006; Mekuye and Abera, 2023). NMs can be categorized in different ways based on their origin, structural configuration, pore diameters, potential toxicity etc. (Santos et al., 2015; Findik, 2021; Joudeh and Linke, 2022). Based on origin, they are classified into natural and artificial NMs (Cho et al., 2019). Natural NMs can be found in diverse forms in nature, including viruses, natural colloids like milk and blood, minerals like clay and fog, gelatin, mineralized natural materials like shells and corals, spider silk, volcanic ash etc. Artificial NMs, such as carbon nanotubes (CNTs) and semiconductor NMs like quantum dots, are manufactured consciously using precise mechanical and manufacturing processes (Cho et al., 2019; Mekuye and Abera, 2023).

Depending on their structural configuration, four basic categories of NMs can be distinguished. They are organic/dendrimers, inorganic, carbon-based, and composite (Zhang et al., 2016; Khan et al., 2019a; Gu et al., 2022). On the nanoscale, organic compounds are converted into organic NMs, which includes liposomes, micelles, ferritin etc. The surface of a dendrimers is coated with numerous chain ends that can perform specific chemical reactions. Typically, inorganic NMs are of two types, metal-based and metal oxide-based NMs. Destructive or constructive methods can be used to create metal-based NMs. Metals such as aluminum, cadmium, cobalt, copper, gold, iron, lead, silver, and zinc are commonly utilized in the synthesis of NMs (Khan et al., 2022a). Metal oxide NMs, are composed of positive metallic ions and negative oxygen ions. Examples of metal oxide NMs that are frequently synthesized and used include silicon dioxide (SiO₂), titanium oxide (TiO₂),

zinc oxide (ZnO), and aluminum oxide (Al₂O₃). These NMs exhibit remarkable properties compared to their metal analogs (Khan et al., 2022a). The five major components of carbon-based NMs are CNTs, graphene, fullerenes, carbon nanofiber, and carbon black. Fullerenes, also known as bucky balls, are spherical structures made up of 28–1500 carbon atoms. The diameter of a single layer can reach to a size of 8.2 nm, while the diameter of a multi-layered fullerene can range from 4 to 36 nm (Mekuye and Abera, 2023). Composite NMs are synthesized by mixing NMs with other NMs, or with large scale materials or with bulk-type materials (Gu et al., 2022).

3. Nanotechnology and plants

NMs have the capability to easily penetrate plant cells, interact with cell membranes, and potentially penetrate cellular structures. Such interactions may activate signaling pathways or disrupt the regular activities of proteins or enzymes responsible for phytohormone synthesis or response (Nadiminti et al., 2013). It helps in assessing the potential risks posed by such pollution and devising strategies to mitigate its adverse effects on plant life. The NMs at an elevated level act as cofactors of different enzymes forming intermediate metabolites and severely affects the plant growth and crop yield (Chai et al., 2013). Various studies have been carried out on the toxic effect of NMs on different plant species including *Lactuca sativa*, *Raphanus sativus*, *Brassica napus*, *Cucumis sativus*, *Zea mays*, *Triticum aestivum*, *Oryza sativa*, *Nicotiana tabacum*, etc. (Hong et al., 2015; Tripathi et al., 2017).

The interaction of various types of NMs with different plant species may vary depending upon the nature, uptakes, translocation of NMs in plant tissues and behaviour or tolerance by plant species towards NMs exposure (Aslani et al., 2014; Wang et al., 2023; Gayathiri et al., 2024; Shaikh et al., 2024; Shinde et al., 2024). More importantly, NMs can have variable impacts on different phytohormones in the same plant. The studies conducted by Hao et al. (2016) revealed that exposure of rice plants to hollow multiwalled CNTs (MWCNTs), Fe-Cobalt (Co)-filled CNTs and Fe-filled decreased the concentrations of IAA (Indole-3-Acetic Acid), GA1, GA3 and isopentenyl adenosine (a type of CK). CNT treatment also decreased the biomass of roots and shoots, root length and shoot height at higher doses, indicating that CNTs inhibit plant growth through down-regulation of growth-promoting phytohormones.

Vanková et al. (2017) correlate the physiological status of *Arabidopsis* with the hormonal profile under the exposure of metal oxide-based NMs. They determined the content of five main phytohormones (auxins, CK, JA, ABA and SA) in shoot apices, leaves and roots after exposure of the plant to ZnO NMs (Zinc Oxide NMs). The concentration of all phytohormones were found to be up regulated up to the mild concentration of ZnO NMs in *Arabidopsis* as compared to higher concentration. Rajae Behbahani et al. (2020) conducted an *in vitro* experiment to investigate the nano-selenium mediated changes in phytohormone content and observed that nano-selenium stimulated root development and embryo-like structures formations during the callogenesis/organogenesis of *Momordica charantia* (*M. charantia*). The nano-selenium mediated changes in auxin, CK and ABA phytohormones through NO/H₂S signaling might be responsible for the differential callogenesis or organogenesis observed in this experiment. They have suggested that the inhibition of xylem tissue differentiation, stem bending, inhibition of primary root development, and appearance of adventitious roots in *M. charantia* indicated hormonal changes (especially ET and auxin) under nano-selenium exposure.

Van et al. (2016) conducted a study with Bt-transgenic and non-transgenic cotton exposed to 0, 100 or 1000 mg L⁻¹ Fe₂O₃ (Iron Oxide NM) NMs and they reported significant differences in the levels of IAA, ABA and GA across the two genotypes upon NM exposure. Fe₂O₃ NMs of 100 mg L⁻¹ concentration increased the IAA level in leaves of both plant types, while no change was observed on application of 1000 mg L⁻¹ Fe₂O₃ NMs. Treatments with both concentrations of Fe₂O₃

NMs decreased the ABA content in conventional cotton but did not influence ABA levels significantly in the leaves of Bt-transgenic cotton. GA content was reduced in non-transgenic cotton leaves for both Fe₂O₃ NM treatments, whereas their levels were significantly increased in the leaves of Bt-transgenic cotton. These findings suggested that GM plants might respond differently to NMs with respect to the level of phytohormones accumulated in them. It is important to highlight that the change in phytohormone level upon exposure of plants to NMs can also be tissue-specific. In addition, cross-talk of phytohormones with other signaling cascades in plants during the NP interaction requires further research. Modern-day molecular techniques can be employed to discover the molecular basis of such complex relationships. The research in this area holds immense potential to provide effective ways for improving plant productivity and stress tolerance mediated by phytohormones. NMs can mediate stress responses in plants by induction or suppression of stress-related phytohormones. NMs in optimum concentration have the potential to modulate the transcription of involved in the synthesis of phytohormones and activation of antioxidant machinery in plants (Fig. 1).

4. Impact of NM pollution on various phytohormones signaling networks

Phytohormones play a crucial role in coordinating different aspects of plant growth and development. Despite their importance, the impact of phytohormones on NM pollution is an underexplored area, as emphasized by Sonkar et al. (2021). It is noteworthy that, despite their crucial roles, phytohormones have not received extensive attention in the context of plant-NM interactions, with only limited recent contributions in this area. Fig. 2 illustrates the proposed mechanisms of NM induced phytohormone modulation under toxic levels of NM in plants.

When plants are exposed to NMs, the plant's phytohormone responses are affected by the degree of stress imposed by the NMs. This involves regulating the signaling process, modifying the quantity of ac-

cessible phytohormones by influencing the available phytohormone pool, and managing the biosynthesis of specific phytohormones. A better understanding of the effects of NMs on regulatory effects of phytohormones can help to assess their toxicity in plants (Table 1). According to existing literature, the relationship between NMs and multiple phytohormone pathways is not linear. Rather, it is characterized by an intricate network of interactions among various phytohormone signaling pathways, involving substantial metabolic crosstalk and reciprocal control points. The regulatory impacts of various phytohormones on NM exposure are discussed in the following section. The regulatory effects and molecular changes of various important phytohormones on plant developmental processes upon exposure to NMs are summarised in Fig. 3.

4.1. Impact of NMs on auxin

Auxin play crucial regulatory role in regulating various plant developmental processes (Gui et al., 2015; Xiong et al., 2021). Studies conducted recently have demonstrated that exposure to NM can affect the control of auxin production and transport, which in turn can affect plant development. Specifically, in *A. thaliana* plants, exposure to ZnO NMs led to inhibitory effect on the concentration of IAA in the root apices, suggesting a regulatory response in auxin levels due to NM exposure (Vanková et al., 2017). Analogously, Sun et al. (2017) evaluated the alterations in the auxin content from silver NM treated roots of *A. thaliana*. Severe inhibition of root gravitropism and substantial attenuation of auxin receptor-related transcripts were observed (such as in *AFB1*, *AFB2* and *TIR1*), indicating a disruption in auxin activity within growing roots. They proposed that the uptake of silver NMs by plants could be transported from cell-cell via the plasmodesmata which interfere by inhibiting the binding of auxin with its receptor.

Another study investigated the pattern in the expression of genes related to signaling mediated by auxin in *A. thaliana* exposed to CuO (Copper Oxide) NMs (Wang et al., 2016). They demonstrated a decrease

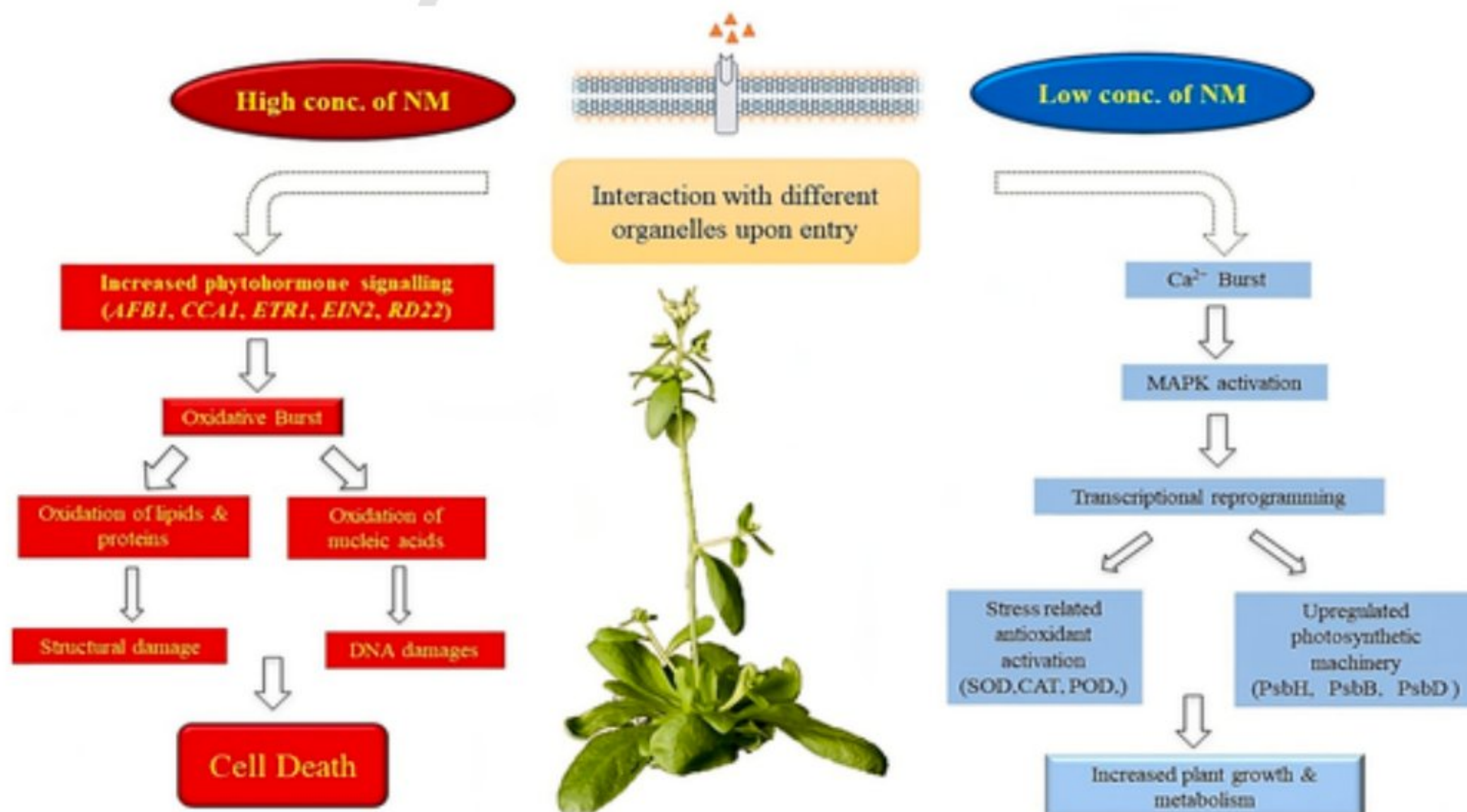


Fig. 1. Schematic diagram illustrates the proposed molecular mechanisms induced by optimum and above optimum concentration of NMs due to phytohormone modulation and oxidative burst in plants. NM, nanomaterial; ROS, reactive oxygen species; SOD - superoxide dismutase; CAT - catalase; POX - peroxidase. The figure highlights the effect of low and high concentration NM exposure followed by signal perception, signal transduction, downstream signaling, transcriptional factor activation, gene expression, protein synthesis and hormonal modulation. *AFB1* & *CCA1* - Auxin signaling genes; *ETR1* & *EIN2* - Ethylene signaling genes; *RD22* - Abscisic acid signaling gene, PsbH, PsbB & PsbD - Photosystem II reaction centre protein subunits.

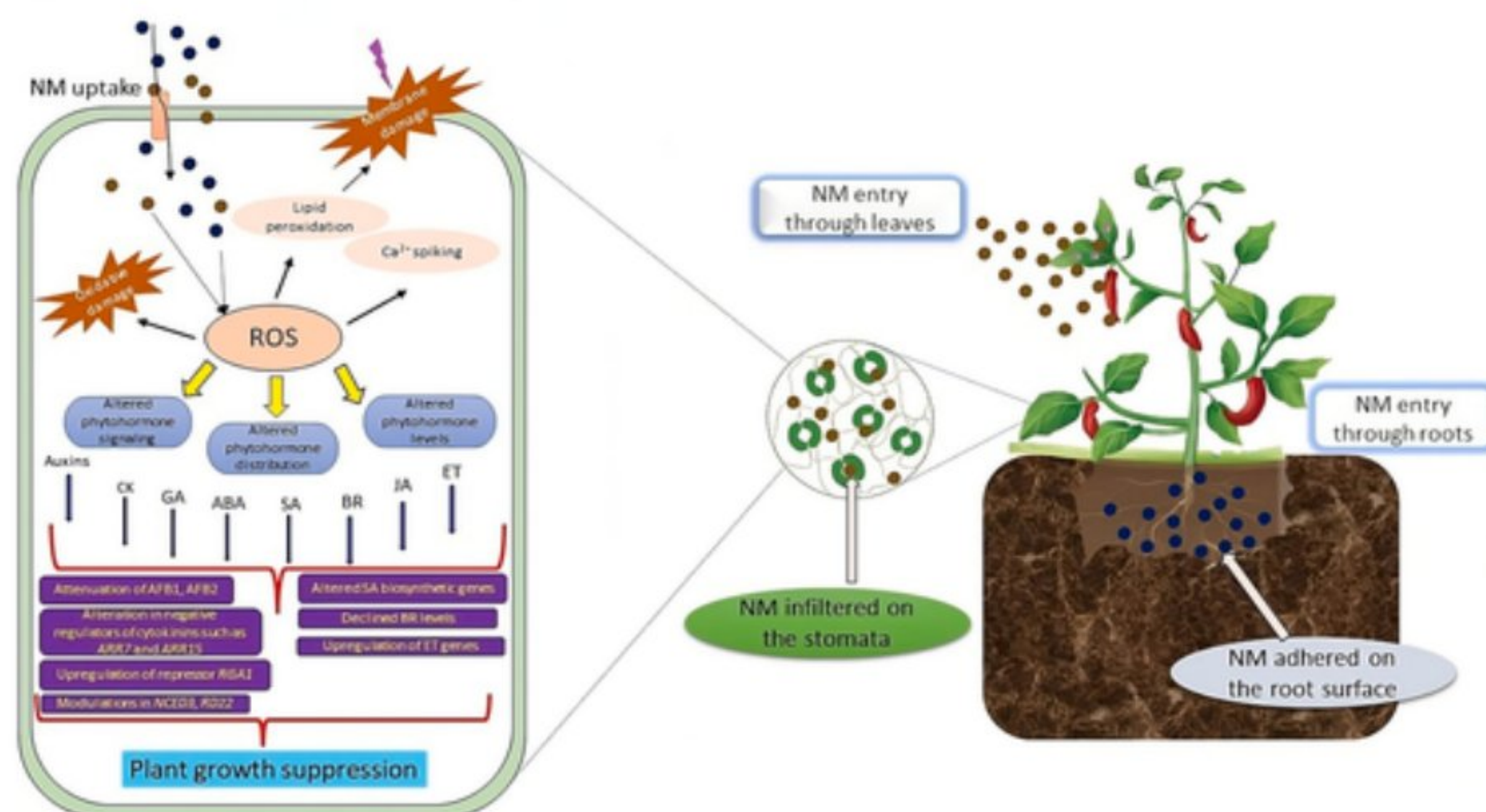


Fig. 2. NMs induced phytohormone modulation under toxic levels of NM in plants. NM entry through plant leaves and roots causes modulations in phytohormone levels through differential signaling mechanism, resulting in detrimental plant growth. NM, nanomaterial; ROS, reactive oxygen species; CK, cytokinins; GA, gibberellins; ABA, abscisic acid; SA, salicylic acid; BR, brassinosteroids; JA, jasmonic acid; ET, ethylene.

in the expression of the auxin signaling F-box protein, which is involved in negative feedback regulation in auxin signaling. A reduction in the expression of the auxin signaling F-box protein, which is involved in the control of auxin signaling via negative feedback, was observed by them. Much like the control of root hair advancements by auxin signaling through the expression of *AXR2/IAA7*, *AXR3/IAA17*, and *SLR1/IAA14*, Wang et al. (2016) observed an increased expression of these three genes in *A. thaliana* when exposed to CuO NMs. In the pursuit of comprehending the intricate physiological and metabolic processes by which CuO NMs influence *Lactuca sativa* (L.), Xiong et al. (2021) conducted a comparative transcriptome analysis, which revealed the adverse impact of the NM on photosynthetic machinery, higher production of reactive oxygen species along with upregulation of auxin transport genes.

4.2. Impact of NMs on CK

Several studies have demonstrated that the CK hormone regulates numerous aspects of plant growth in response to NM action (Tumburu et al., 2015; Vinković et al., 2017; Azhar et al., 2021). Furthermore, Azhar et al. (2021) conducted an analysis of phytohormone signaling in *A. thaliana* in the presence of various metallic NMs (such as ZnO, SiO₂, and ZnO/SiO₂ composite NMs). The study revealed that the accumulation of NM in plant tissues, induced alterations in the expression levels of genes associated with the CK signaling pathway, specifically the negative regulators of CK signaling, *ARR7* and *ARR15*. This underscores the significance of CK in the plant's adaptive response to NM exposure. Tumburu et al. (2015) discovered that 12 days of exposure to TiO₂ or CeO₂ NM (Cerium Oxide NM) altered 346 genes located at the At4g11190 locus in *A. thaliana*, which regulates CK metabolism and a number of defense-related processes.

Vinković et al. (2017) have carried out an ultra-high performance liquid chromatography electrospray tandem mass spectrometry-based hormonal analysis which unveiled, a substantial augmentation in the overall concentration of CK within the *Capsicum annuum* (L.) foliage that had been subjected to citrate coated silver NM treatment at a concentration of 1 mg L⁻¹ when compared to the control. The impact was

detrimental causing a decrease of plant height and biomass among pepper plants along with the excessive production of CK derivatives.

4.3. Impact of NMs on GA

Several studies have shown the regulatory impact of NMs on GA in plants (Hao et al., 2016; Sheteiwiy et al., 2017). Kumar et al. (2018) scrutinized the influence of CNT [such as hollow MWCNTs, iron-filled CNT (Fe-CNTs), and iron-cobalt-filled CNT (Fe Co-CNTs)] on the flowering and photomorphogenesis in *A. thaliana* to highlight the impact of NM exposure in GA metabolism, which revealed a 1.7-fold upregulation in the repressor gene *RGA1* (*REPRESSOR OF GIBBERELLIC ACID 1*). The presence of these CNTs significantly hindered the development of rice plants by decreasing the amounts of endogenous phytohormones by several folds. The study revealed that exposure of *A. thaliana* not only led to reduced levels of GA1, and GA3, but also IAA. Increased concentrations of CNTs led to a reduction in biomass, as well as reduced root and shoot length. Additionally, a decrease in JA, BR, and ABA levels were also noted, potentially diminishing the plant's tolerance to CNT exposure.

4.4. Impact of NMs on ABA

The expeditious reaction of the ABA signaling mechanism in plants due to the presence of NMs have been evidenced in several investigations carried out by Zahedi et al. (2019). Selenium NM-treated strawberry plants showed greater ABA levels especially in saline stressed conditions (Zahedi et al., 2019). In a study conducted by Syu et al. (2014), exposure of *A. thaliana* seedlings to Ag NMs led to increased levels of oxidative stress and subsequent changes in root development patterns. These observed alterations coincided with the upregulation of two specific genes: *NCED3* and *RD22*. *NCED3* is responsible for encoding the enzyme 9-cis-epoxycarotenoid dioxygenase, which is essential for ABA production. *RD22*, on the other hand, encodes a dehydration-responsive protein regulated by ABA.

In a distinct investigation, the influence of silver NMs on the physiological attributes of *Triticum aestivum* under salt stress conditions was

Table 1
Effect of NMs in plants with their possible disruptive impacts on various phytohormones.

Sl. No.	Nanomaterial (NM)	Name of plant	Response	References
1.	ZnO NM	<i>Arabidopsis thaliana</i>	Suppress the growth by decreasing growth promoting hormones auxin and CK in shoot apical meristems, up-regulation of ABA, mainly in shoot apical meristems and leaves, stimulation of SA in leaves and roots, decline in JA as well as its active metabolite jasmonate isoleucine.	Vanková et al. (2017)
2.	Ag NM	<i>Arabidopsis thaliana</i>	Inhibit the expression of auxin receptors, generating a reduction in the accumulation of auxins in the roots	Sun et al. (2017)
3.	CuO NM	<i>Gossypium hirsutum</i>	Inhibit the growth, development, nutrient content, IAA and ABA concentrations.	Le Van et al. (2016)
4.	Graphene oxide NM	<i>Brassica juncea</i>	Decrease in IAA and GA content, reduce the transcript abundance of <i>steroid 5-alpha-reductase (DET2)</i> and <i>isochorismate synthase 1 (ICS)</i> , which are associated with BR and SA biosynthesis, enhance the transcript abundance of <i>brassinosteroid insensitive 1-associated receptor kinase 1 (BAK1)</i> , <i>cam-binding protein 60-like G (CBP60)</i> and <i>calmodulin binding protein-like protein 1</i> , which are associated with BR and SA biosynthesis, increase the transcript abundance of <i>1-aminocyclopropane-1-carboxylic acid synthase 2 (ACS2)</i> , which is associated with ET pathway.	Xie et al. (2020)
5.	TiO ₂ NM	<i>Triticum aestivum</i>	Decrease in IAA, indole propionic acid and JA levels and increase in ABA content.	Jiang et al. (2017)
6.	Green metallic NM	<i>Arachis hypogaea</i>	Decrease in IAA and modification in fatty acid composition.	Santos-Espinoza et al. (2021)
7.	CuO NM	<i>Arabidopsis thaliana</i>	Disruption of JA pathway.	Soria et al. (2019)
8.	CeO ₂ NM	<i>Phaseolus vulgaris</i>	Alteration in secondary metabolism with potential involvement of BRs in both roots and leaves.	Salehi et al. (2019)
9.	Thin-walled carbon nanotubes	<i>Oryza sativa</i>	Decrease the concentrations of ABA, BR, and JA in rice roots and rice shoots and the CNTs had stronger negative effects on JA concentration than on ABA and BR concentrations.	Hao et al. (2016)
10.	ZnO, SiO ₂ , and ZnO/SiO ₂ composite NM	<i>Arabidopsis thaliana</i>	Induce the expression of ET response genes and reduce the expression of cytokinin response genes; alteration of cytokinin signaling pathway related genes (ARR7 and ARR15) expression level.	Azhar et al. (2021)
11.	CeO ₂ NM	<i>Brassica chinensis</i>	Down-regulate 5 photosynthesis genes and 28 auxin-activated genes.	Hong et al. (2023)
12.	CeO ₂ NM	<i>Gossypium hirsutum</i>	Decrease in Zn, Mg, Fe and P nutrient levels of xylem sap, IAA and ABA concentrations.	Nhan et al. (2015)

Table 1 (continued)

Sl. No.	Nanomaterial (NM)	Name of plant	Response	References
13.	Ag NM	<i>Brassica rapa ssp. rapa</i>	Increase in anthocyanin, malondialdehyde, reactive oxygen species production and DNA damage and down-regulates the carotenoid gene expressions.	Thiruvengadam et al., 2024
14.	ZnO NM	<i>Oryza sativa</i>	Higher concentration of hydrogen peroxide and superoxide radical, ABA content increased and GA content was decreased.	Sheteiwy et al., 2017

investigated, with a particular emphasis on quantifying the elevated ABA content, as documented by Wahid et al. (2020). The presence of salinity stress leads to a reduction in ABA levels in response to silver NMs in wheat. Additionally, Yue et al. (2017) elucidated alterations in the ABA signaling pathway resulting from the exposure of maize seedlings to lanthanum oxide (La₂O₃) NMs. Both the roots and shoots of maize seedlings exposed to La₂O₃ NM exhibited a substantial increase in ABA content. This enhanced ABA concentration promptly engaged the ABA receptor, thereby triggering the ABA signaling cascade. Two cultivars of *Oryza sativa* exposed to ZnO NMs have also shown a substantial alteration in the ABA content (Sheteiwy et al., 2017). The transcript levels of genes related to ABA synthesis and catabolism (*OsNCED1* and *OsABA8ox2*) were shown to be modified by NM treatment in both cultivars. Gui et al. (2015) revealed that the roots of both transgenic and non-transgenic rice showed an increase in the levels of IAA and ABA in response to Fe₂O₃ NMs.

4.5. Impact of NMs on ET

The study conducted by Azhar et al. (2021) revealed an extensive analysis of the impact of ZnO NMs, SiO₂ NMs, and a composite of ZnO/SiO₂ NMs on the ET signaling pathway in *A. thaliana*. After being exposed to these NM, the researchers assessed the expression levels of several ET-related genes, including *ETR2* and *ERF1*, which are involved in the ET signaling pathway, and *ACS* and *ACO*, which are involved in ET biosynthesis. A notable increase in the expression of all ET-related genes was identified, suggesting that ZnO NM could potentially accelerate the onset of senescence. In contrast to ZnO NMs, ZnO/SiO₂ composite NMs demonstrated a significantly declined level of transcript expression in ET-regulated genes.

The potential of silver NM to modify the expression of *ACS* gene linked to ET signaling in tobacco plants were examined by Sarmast et al. (2015) through qRT-PCR analysis in *Tecomella undulata* seedlings, exposed to 50 µg mL⁻¹ Ag NMs. The Ag NM caused a decrease in the expression of pivotal ET signaling genes, namely *ETR1*, *ERS1*, and *CTR1* (*Constitutive Triple Response 1*), along with a downregulation of *ACS2*, a crucial downstream gene involved in ET synthesis. This unequivocally establishes that the observed enhancement in root length in response to silver NMs may be attributed to the Ag NM-induced suppression of ET signaling genes.

The study conducted by Wang et al. (2017) revealed a notable increase in the expression of ET-related genes in cucumber plants when exposed to silver sulphide NMs (*Csa6M318160*, *Csa4M001970*, *Csa3M164580*, *Csa3M878200*, *Csa7M405830*, and *Csa2M070880*). Similarly, Khan et al. (2019b) observed elevated expression of specific genes associated with ET signaling (*ETR1*, *EIN2*, and *EIN3*) and biosynthesis (*ACS2*, *ACS5*, *ACS6*, *ACS8*, *ACO1*, and *ACO2*) in *A. thaliana* plants exposed to ZnO NMs. Moreover, the application of ZnO NM treatment led to an increase in endogenous ET levels, suggesting a disruption in the development and growth of *A. thaliana*.

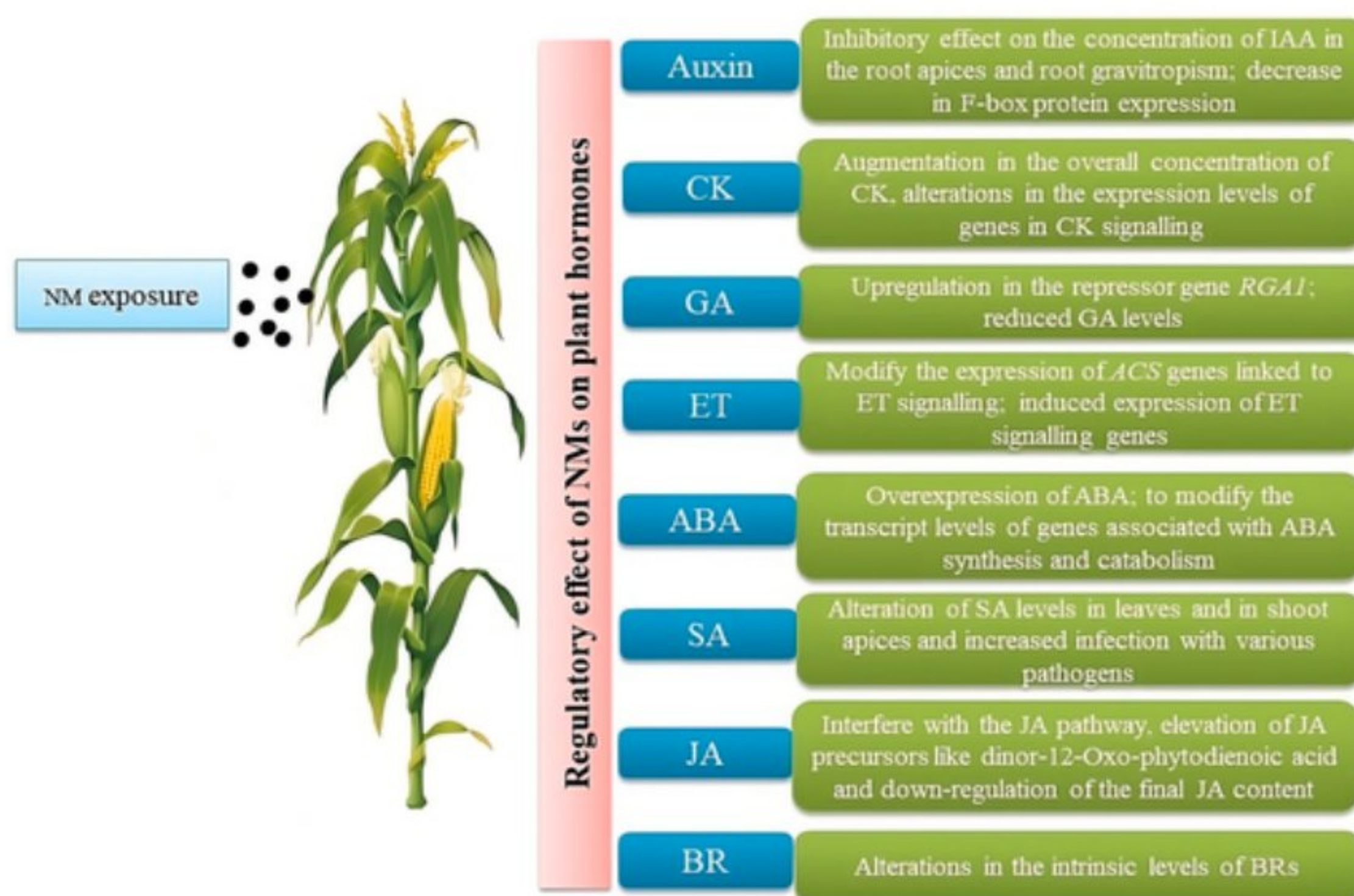


Fig. 3. The regulatory effects and molecular changes of various important phytohormones upon exposure to NMs in plants. NM, nanomaterial; IAA, indole-3 acetic acid; *RGA1*, *Repressor of Gibberellic Acid 1*; *ACS*, *1-Aminocyclopropane-1-Carboxylic Synthase*.

4.6. Impact of NMs on SA

Numerous studies have highlighted the impact of NMs on endogenous SA levels in plants. Vanková et al. (2017) observed a notable rise in SA concentration in the leaves of *A. thaliana* following exposure to ZnO NMs. Conversely, in the roots, a significant increase in SA levels was noted under both moderate and higher concentrations of ZnO NM exposure. Nonetheless, the decrease in shoot apical meristem activity and leaf growth observed under severe NM treatment could be attributed to the antagonistic interplay between SA and ABA arising out of the higher NM exposure. Moreover, contrasting results were noted by García-Sánchez et al. (2015) in *A. thaliana*, wherein application of NM such as TiO₂, Ag and MWCNT to biotically stressed plants, transcriptionally repressed defence response genes especially the SA biosynthetic genes. This led to an increased infection with the pathogen introduced experimentally on the plant. Also, the root hair density and root developmental genes too were drastically inhibited upon NM exposure.

4.7. Impact of NMs on JA

The use of targeted metabolomic platform has provided insights into the effects of various NMs on the JA pathway. The application of CuO NMs on *A. thaliana* has been demonstrated to interfere with the JA pathway, resulting in an elevation of JA precursors like dinor-12-Oxo-phytodienoic acid and down-regulation of the final JA content. An investigation conducted by Soria et al. (2019) revealed that when *A. thaliana* leaves were exposed to CuO NMs, there were notable alterations in many metabolites related with plant defense mechanisms. These changes had an influence on the JA-associated signaling pathway, which is crucial for plant defense signaling pathways. NMs can also influence phytohormone levels in a fashion similar to that induced by mechanical stresses. Angelini et al. (2022) reported increase in the levels of derivatives of three major stress phytohormones JA, ABA and SA in *Arabidopsis thaliana* plants treated with 50 mg L⁻¹ of Ag NMs and that this response resembled the physiological response of the plant to mechanical stress. In a separate study conducted by Hernández-

Hernández et al. (2018), an increase in the expression of genes linked to JA and antioxidative enzymes was observed in 30-day-old tomato seedlings when treated with Cu (Copper) NMs. Additionally, Zhou et al. (2021) investigated the effects of polystyrene NMs (PS NMs) on plant hormone signaling through a microcosm study. They found that in rice roots, the content of phytohormones, particularly JA biosynthesis, was significantly suppressed by PS NMs at a concentration of 100 mg L⁻¹.

4.8. Impact of NMs on BR

Several studies have highlighted changes in the intrinsic levels of BR in plants as a direct response to exposure to metallic NMs. Hao et al. (2016) reported a significant decrease in BR levels, along with other phytohormones such as ABA and JA, in both the roots and shoots of *O. sativa* plants when exposed to CNT NMs filled with ferromagnetic alloys. This resulted in a decreased ability of the plants to cope with stressful conditions. Additionally, Salehi et al. (2019) observed alterations in the secondary metabolism of common beans when exposed to lower concentrations of CeO₂ NMs on both leaves and roots. They noted that the accumulation of Ce in the roots was subsequently transported to the aboveground parts of the plant, leading to tissue-specific metabolic changes. Fig. 4 illustrates the various NMs induced phytohormone disruptive signaling mechanism in plants.

5. Conclusions

This review emphasizes the significant influence of NMs on phytohormone networks in plants, exposing an intricate interplay that spans across physiological, cellular, and ecological dimensions. The increased production and exposure of engineered NMs pose challenges to plant growth and stress responses, influencing phytohormone biosynthesis and altering signaling pathways. The intricate relationships explored here, involving auxins, CK, GA, ABA, ET, JA, SA and BRs shed light on the potential disruptive effects on gene transcription and protein/enzyme functions, especially related to phytohormones. Crucial need emerges for further research leveraging modern molecular techniques

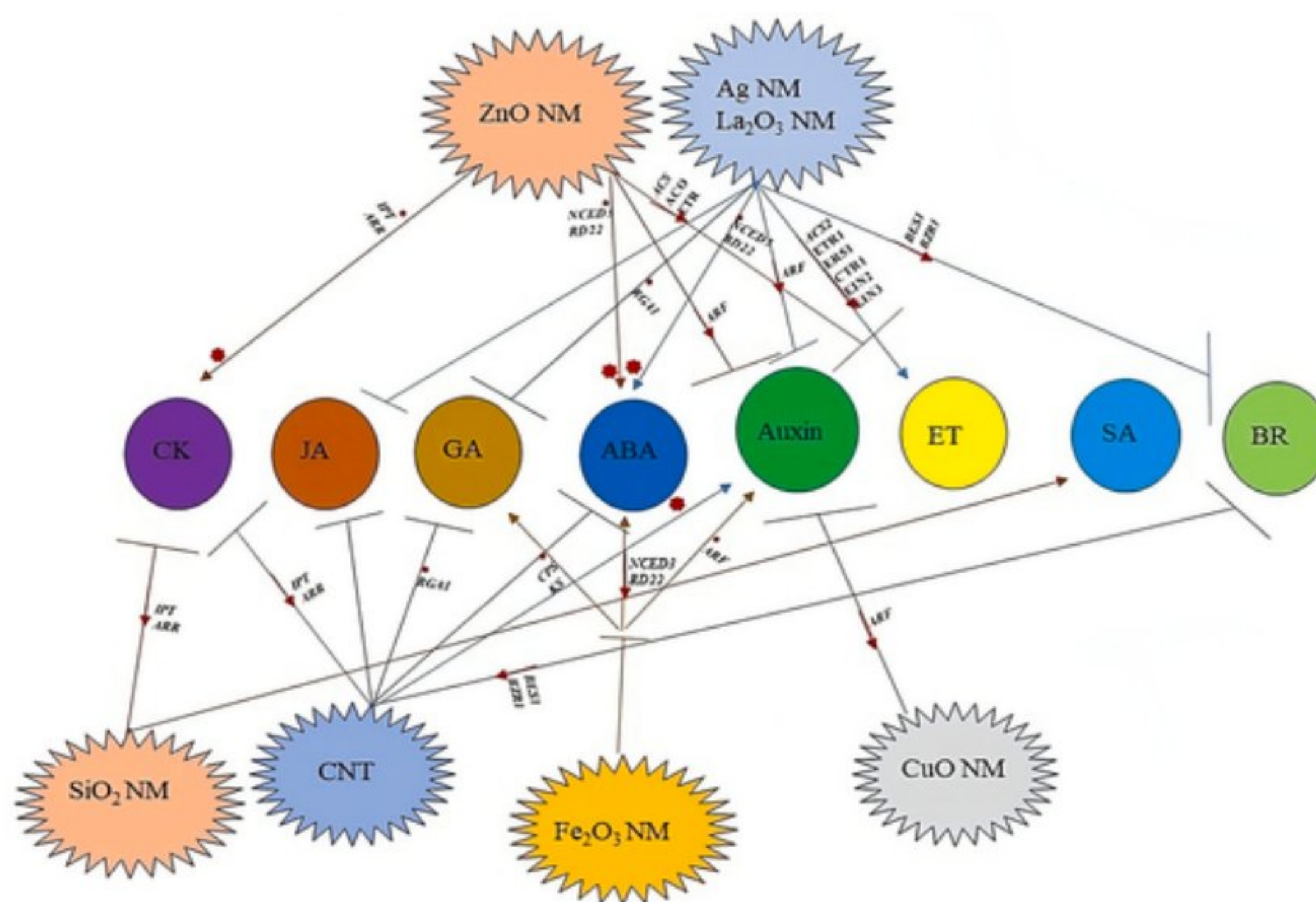


Fig. 4. Various NMs induced phytohormone disruptive signaling in plants. NM, nanomaterial; IPT, Isopentenyl transferase; ARR, Arabidopsis response regulators, RGA1, G-protein alpha subunit; BZR1, brassinazole-resistant 1; BES1, BRI1-EMS-suppressor 1; CPS, Ent-copalyl diphosphate synthase; KS, Ent-kaurene synthase; NCED3, Nine-cis-epoxycarotenoid dioxygenase 3; RD22, Dehydration-responsive gene; ACS, 1-aminocyclopropane-1-carboxylic synthase; ACO, 1-Aminocyclopropane-1-Carboxylic Acid Oxidase; ARF, Auxin response factor; CTR1, constitutive triple response 1; EIN2, ethylene-insensitive 2, ethylene insensitive 2; EIN3, ethylene insensitive 3. Upregulation; Inhibition; Downregulation.

to unravel the nuanced connections between NMs and phytohormones is required. This deeper understanding not only offers insights into enhancing plant productivity and stress tolerance but also highlights the necessity for innovative, environmentally conscious solutions to mitigate the ecological consequences of NM pollution. Although there could be disruption of phytohormone networks by NM, its role in supporting sustainable farming practices cannot be disregarded. Creating NMs that boost growth, increase stress tolerance, or improve nutrient uptake without negatively affecting phytohormone networks could be an alternative approach. One important factor to consider could be to identifying substitutes that offer the same benefits without having serious ecological impact.

Uncited references

CRediT authorship contribution statement

Parammal Faseela: Writing – original draft, Conceptualization. **Joy M. Joel:** Formal analysis, Data curation. **Riya Johnson:** Formal analysis, Data curation. **Edappayil Janeeshma:** Formal analysis, Data curation. **Puthukkollu P. Sameena:** Formal analysis, Data curation. **Akhila Sen:** Formal analysis, Data curation. **Jos T. Puthur:** Writing – review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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