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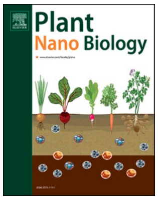

Nano-improved plant salinity tolerance: The importance of K^+/Na^+ homeostasis and crosstalk between Ca^{2+} and hormones

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ABSTRACT

Salinity stress is a major constraint on plant organ morphogenesis, and agricultural production, mostly by disrupting ion homeostasis and plant water status, leading to detrimental K^+/Na^+ imbalance. Maintaining subcellular ionic balance is a critical defense mechanism against abiotic stresses, and plants employ diverse strategies to mitigate ion toxicity. Nanobiotechnology offers a promising approach to enhance plant ion homeostasis under stressed environments, leveraging nanoparticles' (NPs) capacity to modulate stress-responsive signaling pathways in crops. Crucially, NPs initiate crosstalk between Ca^{2+} signaling and hormonal networks, which cooperate with reactive oxygen species (ROS), K^+, and nitric oxide (NO) signaling to regulate transcription factors (TFs) essential for ionic equilibrium. This review examines the role of NPs in promoting K^+/Na^+ homeostasis during salinity stress by regulating molecular, physiological, anatomical, and morphological mechanisms. These NP-induced Ca^{2+}/hormonal networks directly or indirectly regulate NO signaling to bolster organ morphogenesis and stress tolerance. NPs enhance salinity tolerance by upregulating key genes (e.g., *SOS1*, *SOS2*, *SOS3*, *HKT1*, *NHX*), improving ion homeostasis and organ development. Moreover, NP-triggered crosstalk between Ca^{2+} signaling and hormones plays a pivotal role in regulating TFs such as *bHLH*, *R2R3-MYB*, *WRKY*, *NAC*, *ZIP*, *ERFs, and NFX1*. Collectively, these signaling and TF networks orchestrated by NPs sustain a high K^+/Na^+ ratio by regulating K^+ and Ca^{2+} transport/distribution and reducing Na^+ toxicity. Improved K^+/Na^+ regulation enhances nutrient uptake, activates ROS scavenging systems, modulates phytohormone levels, boosts photosynthetic efficiency, and optimizes stomatal motions. Understanding the mechanistic basis of NP-mediated stress regulation will elucidate their mode of action and the associated signaling cascades, clarifying their contribution to ion homeostasis under salinity stress.

1. Introduction

In plants, ion homeostasis —the control of mineral ion levels in cells and tissues—is fundamental for metabolic function. Nutrient imbalance or over-accumulation can cause toxicity, making ion regulation critical for salinity adaptation. Salt stress often causes an imbalance in the uptake, translocation, and distribution of ions, including sodium (Na^+), potassium (K^+), calcium (Ca^{2+}) and chloride (Cl^-) (Abbasi et al., 2016; Mulet et al., 2020; Ran et al., 2022). Stress due to salinity lowers the capacity of plants to uptake water due to high osmotic pressure, which also causes water loss from root cells to the soil under high salt concentrations, leading to plant cell shrinking and dehydration. To avoid dehydration under stress conditions, plants adjust their osmotic potential by maintaining ion homeostasis and accumulating organic

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osmolytes, which allows them to retain water, regulate cell turgor, and minimize toxicity (Chaves et al., 2009; Mohamed et al., 2020a; Shabala and Shabala, 2011). Under salinity stress, the most significant issue for plants is the excessive accumulation of Na^+, which leads to K^+ deficiency and massive energetic costs. High Na^+ levels directly compete with K^+ for entry through shared membrane transporters, while also indirectly limiting K^+ mobility by reducing water uptake. Na^+ ions compete with K^+ ions for binding sites on enzymes and ribosomes, disrupting K^+-dependent processes because Na^+ cannot effectively replace K^+ in these crucial functions. Both ions are alkali metals and share physicochemical similarities, allowing them to bind to the same sites. However, K^+ is essential for activating many enzymes (over 50) and for proper protein synthesis by enabling tRNA binding to ribosomes. High Na^+ concentrations, common under salt stress, can outcompete K^+ for these sites, impairing enzyme function and leading to metabolic disruption (Hasanuzzaman et al., 2018; Wang et al., 2013; Wu et al., 2019). Consequently, a key marker of salinity tolerance is the maintenance of a high cytosolic K^+/Na^+ ratio. Plants achieve this by enhancing the activity and expression of K^+ uptake systems and decreasing Na^+ activity and level within the plant cell cytoplasm (Assaha et al., 2017; Mohamed et al., 2020b; Wu et al., 2018b). In glycophytes, vacuolar Na^+ sequestration (isolating Na^+ within the vacuole) and cellular Na^+ exclusion (pumping Na^+ out of the cell) are the most effective mechanisms to decrease Na^+ activity and level. Regulations of Na^+ transporters and channels such as NHX (Na^+/H^+ exchangers on the vacuolar membrane) help to remove the Na^+ ions from cytoplasm to the cell vacuole and SOS1 (a Na^+ efflux pump located in the cytoplasm membrane belong to salt overly sensitive (SOS) pathway) help pump Na^+ out of the plant cell (Britto and Kronzucker, 2015; Keisham et al., 2018; Wu et al., 2019). Therefore, understanding the regulations of K^+/Na^+ homeostasis during stress through signaling pathway activation and ion transporters or channels to maintain cellular osmotic potential is essential for developing stress resistance strategies in many plants.

Nanoparticles (NPs) represent an innovative technology in boosting plant resilience against various environmental stressors, including salinity stress. One key mechanism involves NPs helping plants maintain ion homeostasis by triggering specific cellular stress-signaling pathways that subsequently activate the function of key ion transporters and channels, enabling plants to better control the uptake, exclusion, or compartmentalization of ions (such as Na^+, Cl^-, K^+) under stressful conditions (A. Singh et al., 2024b; Thabet and Alqudah, 2024). Because NPs are tiny and have a huge surface area, they can enhance the plant's capacity to uptake vital nutrients, decrease the uptake of harmful elements, and activate the antioxidant defense system, encouraging plant cell division and differentiation. According to reports, NPs can improve K^+/Na^+ homeostasis in the salinity-stressed plants in many crops including wheat seedlings by AgNPs (Wahid et al., 2020) and zinc oxide (ZnO) NPs (Lalarukh et al., 2022), safflower plants by ZnO NPs (Yasmin et al., 2021), cotton, rice, and *Arabidopsis* by poly acrylic acid coated nanoceria NPs (PNC) (Liu et al., 2021; Wu et al., 2018a), and rapeseed by ZnO NPs and SeNPs (El-Badri et al., 2021) and by nanozymes of polyacrylic acid-coated Mn_3O_4 NPs (PMO) and PNC (Li et al., 2022a; Liu et al., 2024). NPs in the form of nano-fertilizers can induce the absorption of vital ions that are essential for ion balance and overall plant function, including Ca^{2+}, K^+, and magnesium (Mg^{2+}), while reducing excess uptake of Na^+ ions by altering membrane transporters (Ayyaz et al., 2024; Gupta et al., 2024; A. Singh et al., 2024b).

Plant hormones are key phytomolecules that play pivotal functions in orchestrating the formation of plant tissues and organs with distinct architectures. It has been demonstrated that plant hormones can be modulated by NP application, including AgNPs applied as priming agents in *T. aestivum* L. (Abou-Zeid and Ismail, 2018), AgNPs applied as a foliar agent in *T. aestivum* L. (Wahid et al., 2020), Se NPs applied in the growth medium in *Momordica charantia* (Rajaee Behbahani et al., 2020), Au NPs and SiO NPs applied in the growth medium in *Arabidopsis thaliana* (Azhar et al., 2021; Tiwari et al., 2016), and Fe NPs applied as a priming agent in *Citrullus lanatus* (Kasote et al., 2019). NPs interact with hormone biosynthesis/signaling pathways such as gibberellins (GAs), cytokinins (CKs), auxin (Aux), abscisic acid (ABA), salicylic acid (SA), and ethylene (Eth), though nano-hormone crosstalk mechanisms remain poorly understood. Tripathi et al. (2022) have provided a clear discussion regarding the integrated role of NPs exposure with the role of plant hormones in plant growth regulations under abiotic and biotic stress environments.

NPs can induce Ca^{2+} signaling in plants through a variety of mechanisms, primarily by directly interacting with membrane ion channels or indirectly by generating ROS and activating calcium-dependent signaling pathways that trigger changes in intracellular levels of Ca^{2+} and affect ion channel functions (Germande et al., 2022; Hussan et al., 2024; Li et al., 2022a). NPs may influence the activity of H^+-ATPases and K^+ transporters (e.g., Arabidopsis K^+ transporter 1 (AKT1), K^+ channel in *Arabidopsis thaliana* 1 (KAT1)) by activating Ca^{2+} signaling pathways. Elevated Ca^{2+} levels can promote the activation of these transporters, ensuring proper K^+ uptake and preventing K^+ deficiency under stress conditions (Kumari et al., 2021; Mishra et al., 2024).

The induced Ca^{2+} and hormone signaling by NPs can participate in promoting cellular signaling pathways through their interaction with plant cell components, especially those associated with K^+/Na^+ homeostasis. For instance, the induced Ca^{2+} signaling can promote signaling molecules, including ROS, K^+, and nitric oxide (NO), which in turn can activate or inhibit TFs that control ion transporters or ion channels (Banerjee and Roychoudhury, 2022; Cameron et al., 2022; A. Singh et al., 2024a). The interactions between NPs and these signaling network pathways are complicated and context-dependent, but they generally involve several key mechanisms. Therefore, in this review article, we: (i) decipher the role of NPs in K^+/Na^+ homeostasis via molecular, physiological, anatomical, and morphological mechanisms; (ii) elucidate the pivotal crosstalk between NP-induced Ca^{2+} signaling and hormonal networks in regulating ROS, and NO^- signaling as well as TFs related to K^+/Na^+ homeostasis and cell morphogenesis; (iii) discuss NP-mediated stomatal regulation and identify future research directions in agricultural sustainability.

2. Functions of K^+/Na^+ homeostasis in salinity-stressed plants

2.1. Fundamental roles of K^+/Na^+ homeostasis

The ion homeostasis governs critical processes, including cell turgor maintenance, enzyme activation, stomatal regulation, and synthesis of biomolecules such as chlorophyll. In addition, K^+/Na^+ homeostasis indirectly participates in the maintenance of target anion and cation gradients through the plasma membranes (PMs) to the proper membrane potential. Thus, maintaining K^+/Na^+ homeostasis is a universal biological imperative, with plants evolving specialized transporters (e.g., SOS, high-affinity potassium transporter (HKT)) to combat salinity (Dubyak, 2004; Mulet et al., 2020). In this regard, efficient systems have been developed in plants to maintain a safe level of these elements in the organelles and cytosols of their cells, allowing a continuous developmental process. Plant growth, stress tolerance, and regular physiological functions all depend on the intracellular ionic (K^+/Na^+) balance and homeostasis. Thus, plants use a variety of methods to maintain ion homeostasis, such as ion transport controlled by ion transporters, H^+ pumps, and channels, to maintain an optimum ionic flux and prevent ion toxicity.

2.2. Salinity sensing & rapid signaling

The K^+/Na^+ homeostasis process in plants under salinity stress is a complex dynamic process that often occurs from the early stage of salinity stress sensing and signaling steps and at the steps of plant adaptive responses (Fig. 1). As summarized in Fig. 1, salinity sensing triggers adaptive responses via the rapid Na^+-induced signaling waves,

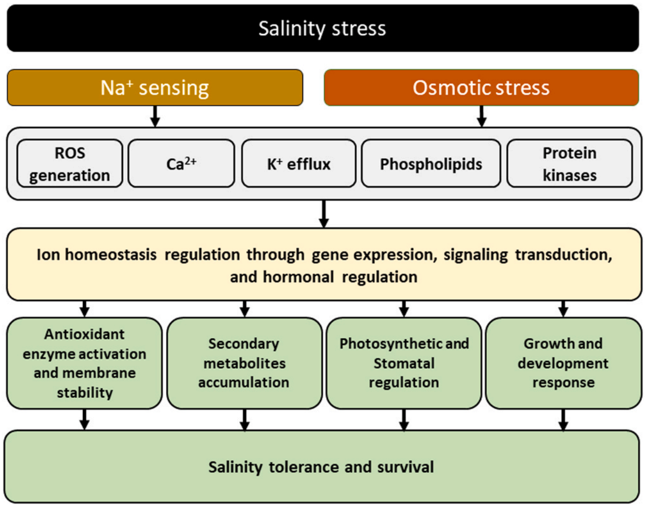

Fig. 1. The flow chart of sensing and signaling processes of salinity stress and role of ion homeostasis in plant adaptive responses to salinity stress conditions from rapid Na^+-induced sensing to tolerance and survival.

mitogen-activated protein kinase (MAPK) signaling, and hormonal signaling transductions (Shabala et al., 2015; Singhal et al., 2021). Rapid Na^+-induced signaling waves refer to the early Na^+ sensing and signaling that occurs through several signals, including Ca^{2+}, K^+, H^+, ROS, phospholipid metabolism, and protein kinase activation before or after Na^+ import and occurs in the cytosol of cells or extracellular. These rapid signaling acts as downstream signals via altering gene expression, biosynthesis of plant hormones and stimulating the transmission of signals, including MAPK and plant hormones. Lastly, the salinity-induced signaling cascade triggers adaptive responses including enzymatic and non-enzymatic antioxidant activations, secondary metabolite accumulations, and photosynthetic and stomatal regulations (Shahzad et al., 2021; Zhao et al., 2015).

Plants detect osmotic shifts extracellularly, intracellularly, and/or via ion transporters in the PMs before Na^+/Cl^- toxicity manifests (Munns and Tester, 2008). Fig. 2 illustrates Na^+ sensing via non-selective cation channel (NSCC)/ glycosyl inositol phosphorylceramide (GIPC) receptors and downstream Ca^{2+}/3',5'-cyclic guanosine monophosphate (cGMP) signaling. Na^+ enters through an NSCC, which is one of the channels that transport Na^+ across PMs into the cytosol. Na^+-induced salt signals activate NSCCs; these signals include Ca^{2+}, ROS and cGMP (Fig. 2). Besides NSCCs, Na^+ ions can enter plant cells through other unidentified channels, resulting in a membrane voltage that depolarizes the membranes (Shahzad et al., 2021). The cGMP is a cyclic nucleotide and is one

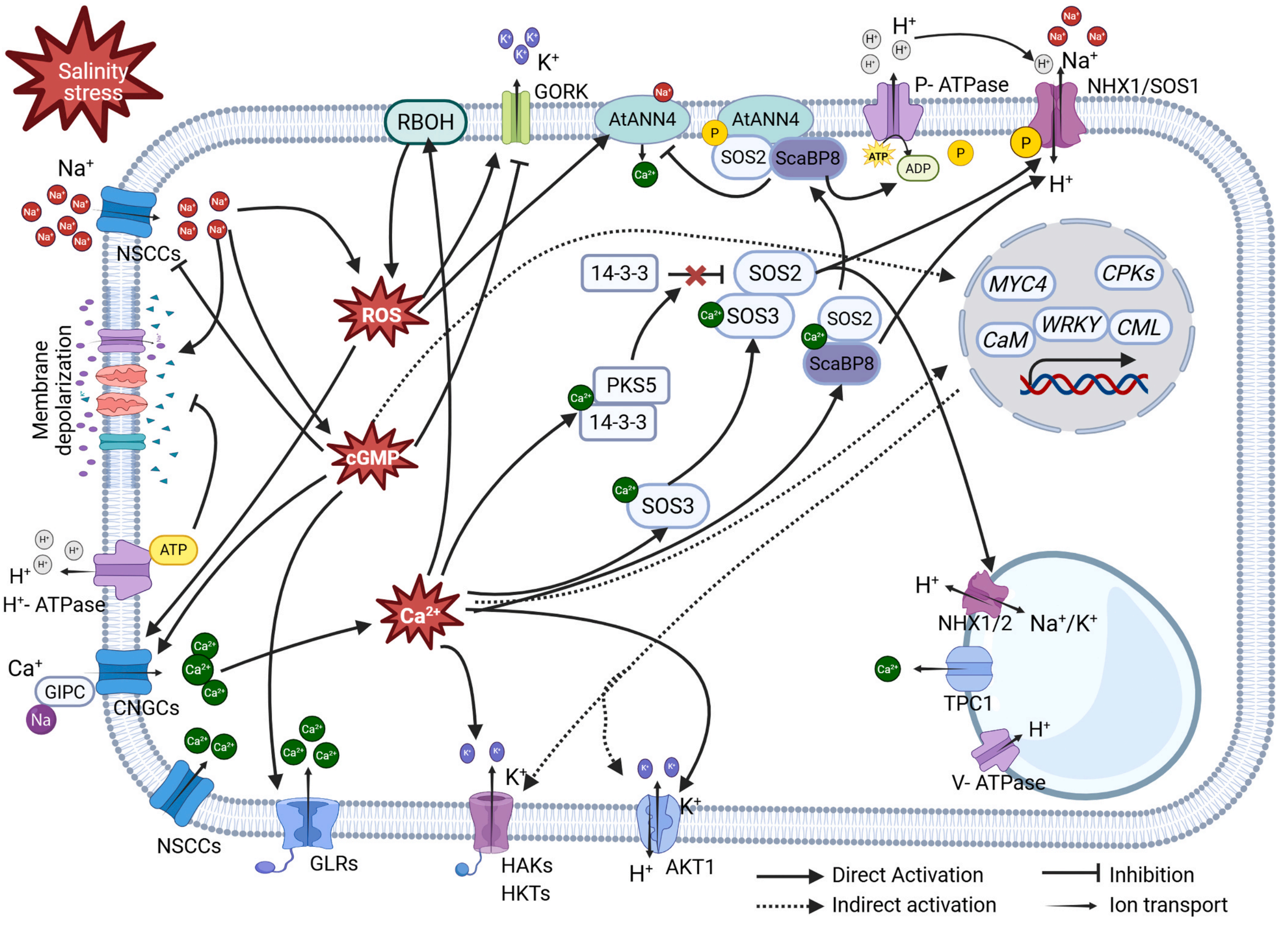

Fig. 2. Na^+ sensing and the role of different signaling concerning K^+/Na^+ homeostasis under salt stress in plants. cGMP; 3',5'-cyclic guanosine monophosphate, GORK; guard cell outward-rectifying potassium efflux channels, SOS1; salt overly sensitive 1, NHX1; Na^+/H^+ exchanger1, PKS5; SOS2-like protein kinase5, CNGCs; cyclic nucleotide-gated channels, RBOH; respiratory burst oxidase homologous, TPC1; two-pore channel 1, V-ATPase; vacuolar ATPase, P-ATPase; plasma membrane ATPase, AKT1; inward-rectifying K^+, HAKs; High Affinity K^+ transporters, CaM; Calmodulin, CPKs; calcium-dependent protein kinases, CML; calmodulin-like protein, GLRs; glutamate receptor-like channels, and *MYC4;* Arabidopsis bHLH transcription factor.

of the early components that are raised by NaCl-induced sensing and signaling. Moreover, this cGMP induces Ca^{2+} import upon exposure to salt stress by activating Ca^{2+} channels, including cyclic nucleotide-gated channels (CNGCs), but some other stresses can induce this process. The cellular cGMP increase might be observed within a few seconds after the application of osmotic stress or salt stress, resulting in inhibition of Na^+ uptake, possibly via CNGCs and glutamate receptors (GLRs). It has roles in regulating the transcription of genes involved in promoting K^+ uptake (Isayenkov and Maathuis, 2019; Isner and Maathuis, 2018; Liu et al., 2023a). Recently, GIPC sphingolipids have been functionally identified as Na^+ receptors for sensing apoplastic Na^+ in the plasma membrane (PM) and have an additional role in gating Ca^{2+} influx channels, such as CNGCs (Jiang et al., 2019; Yu et al., 2020).

2.3. Downstream signaling & adaptive responses

Under salinity stress conditions, several downstream signaling and adaptive responses are activated in plants. Ca^{2+} signaling is one of the signaling that occurs as earliest waves induced by salt stress. As a second messenger, Ca^{2+} plays several important roles in ion homeostasis by stabilizing cell membranes and cell walls, besides relaying the salt stress signal from cell surface receptors to initiate a downstream response to the effector proteins. In addition, Ca^{2+} is a vital nutrient for plants, and it is necessary for the control of physiological functions, including elongation of root hair, movement of stomatal guard cells, and growth of pollen tubes (Lohani et al., 2020; White and Broadley, 2003). Quick Ca^{2+} waves occur in the cytosolic as a downstream signaling in response to the binding of Na^+ ions to GIPCs through CNGC1 or through an unknown Ca^{2+} channel (Fig. 2). Rapid Ca^{2+} waves that are unique to Na^+ are typically identified in *A. thaliana* root, and this response is a subsidiary of the vacuolar ion channels TPC1; Two-Pore Channel1, that facilitates the vacuole's release of Ca^{2+}; consequently, the speed of long-range Ca^{2+} signaling in *tpc1* mutants has been drastically reduced. Evidence has been provided that the Ca^{2+} wave/TPC1 system may help plants tolerate stress overall and probably causes systemic molecular reactions in target organs (Jiang et al., 2019; Wang et al., 2014).

Recently, calmodulin (CaM), calmodulin-like (CML), Ca^{2+}-dependent protein kinase (CDPK/CPK), and calcineurin B-like (CBL) proteins have been identified as regulators in Ca^{2+} signaling-related pathways. Primary Ca^{2+} sensors, CaM and CML proteins, have been reported to participate in the regulation of stress responses, including salinity stress and the regulations of plant development. CaM and CML can convert Ca^{2+} signaling into several levels of transcriptional response, protein phosphorylation, or metabolic responses. CaMs are conserved proteins that bind Ca^{2+}, and usually have four EF-hand motifs and 149 residues, containing two alpha-helices in each EF-hand linked by a loop of 12 amino acids and residues (He et al., 2020; Lohani et al., 2020; Xue et al., 2023). CBLs can bind Ca^{2+} and cause protein phosphorylation to control Ca^{2+} flux output through interacting with CBL-interacting protein kinase (CIPK) (Bender et al., 2018; Tang et al., 2020). The pathway of salt overly sensitive (SOS) has been well characterized. First, Ca^{2+} is sensed after the binding between SOS3 (also known as CBL4). Second, SOS3 interacts with SOS2/CIPK24 by binding SOS3 to SOS2 as a Ca^{2+} sensor element, forming the SOS2-SOS3 complex. Third, the SOS2-SOS3 complex can phosphorylate the SOS1/NHX7 (sodium/hydrogen exchanger 7), which can promote the movement of Na^+ out of the stressed cell, as presented in Fig. 2 (Liu et al., 2015). In an additional pathway, 14–3–3 protein and SOS2-like protein kinase 5 (PKS5) mediate SOS2 activity. PKS5 can phosphorylate SOS2 and repress SOS2 activity by inducing binding to 14–3–3 proteins under normal conditions. During salt stress, Ca^{2+} binds to 14–3–3 proteins, which repress PKS5 activity, indicating that Ca^{2+} might modulate SOS2 activity through an alternative pathway. Moreover, salt stress-induced Ca^{2+} level is mediated by AtANN4 (a Ca^{2+}-binding annexin that acts as an early sensor of salt stress) that binds to the PM in response to salt-induced phospholipid changes, forming salt-specific Ca^{2+} signals. The initial Ca^{2+} spike activates Ca^{2+} sensors (including SOS3/CBL4 and SCaBP8/CBL10), which can bind and activate SOS2 kinase. AtANN4 can be phosphorylated by the activated SOS2 at specific residues, inhibiting AtANN4's channel activity and reducing further Ca^{2+} influx, generating a salt-specific signal for activating Na^+ extrusion by SOS1 Na^+/H^+ antiporter regulation (Van Zelm et al., 2020). CDPKs/CPKs are a kind of vital regulatory protein of Ca^{2+} sensing machinery, which is triggered by various environmental and developmental stimuli. Ser/Thr protein kinases that exhibit kinase activity inside a single protein are known as CPKs (Zhang et al., 2014).

Salt stress rapidly elevates apoplastic ROS (e.g., $O_2^{\bullet-}$, $OH^{\bullet}$, H_2O_2, and $^1O_2$), disrupting redox homeostasis. Despite their destructive nature, ROS is a second messenger that is involved in numerous cellular processes, including ion homeostasis. Moreover, ROS react with membrane proteins, lipids, carbohydrates and DNA, which is controlled by different mechanisms of antioxidant defence systems (non-enzymatic and enzymatic) (Ahmad et al., 2009; Liu and He, 2016; Sharma et al., 2012). Plant nicotinamide adenine dinucleotide phosphate (NADPH) oxidases, another name for respiratory burst oxidase homologous (RBOH) proteins, are enzymatic ROS-generating systems found in the PM system in many plants. The complex ROS generation network is continuously active and plays a key role during the rapid response to salt stress, as evidenced by the dynamic changes in the expression patterns of the 10 RBOH genes (RBOHA-RBOHJ) in *A. thaliana*, which produced ROS waves for 24 h (Chen and Yang, 2019; Van Zelm et al., 2020).

Through phosphorylation, the MAPK signaling transduction cascade can integrate multiple downstream mediators of stress-responsive genes in stressed cells (Lohani et al., 2020). Therefore, the components of MAPK signaling are represented as assembly spots involved in multiple functions to activate stress resistance mechanisms. MAPK signaling in conjunction with Ca^{2+} ion signaling quickly synthesizes the included evidence for the adaptation of the response of cells to external stressors, such as salinity stress (Cristina et al., 2010; Makavitskaya et al., 2018; Mohamed et al., 2022). Several studies indicated that *MPK6* has an axis function that dynamically controls the accumulation of the signaling component of ROS (Golldack et al., 2014). The TFs of the *WRKY* family (as a MAPK signaling) have participated in how plants grow and react to biotic and abiotic stressors. Earlier reports announced that the *WRKY* TFs varied greatly in response to salt stress as well as several regulatory functions in salt resistance in crops (Bo et al., 2020; Ullah et al., 2018; Wu et al., 2017; Yan et al., 2014). *MYC4* (Arabidopsis *bHLH* transcription factor) in *Gossypium hirsutum*, which can combine with JAZ (Jasmonate ZIM-domain) to inhibit the expression of downstream genes promoting the cis-element G-box, influencing salinity resistance (Zhao et al., 2020a).

3. Role of plant hormone signaling in K^+/Na^+ homeostasis

Plant hormone regulation and K^+/Na^+ homeostasis are closely linked, as both are essential for maintaining proper cell division and expansion under environmental stresses (Amin et al., 2021; Martínez-Ballesta et al., 2020; Mulet et al., 2020). The role of hormone regulation in maintaining K^+/Na^+ homeostasis is shown in Fig. 3. It has been reported that the plant hormones, Aux, CK and GA can facilitate the uptake of osmolytes such as K^+ ions into the cells, increasing the extensibility of the cell walls and promoting cell division and expansion. In contrast, ABA influences K^+ efflux, especially in response to environmental stress, thereby impacting osmotic potential and stomatal behaviour. Therefore, understanding the crosstalk between plant hormone regulation and ion homeostasis is crucial for developing a novel strategy for improving stress resistance in plants.

3.1. Auxin signaling (Aux)

Auxin plays a modulatory role in salt stress responses by influencing root architecture and ion transport processes. In *Zea mays*, it was

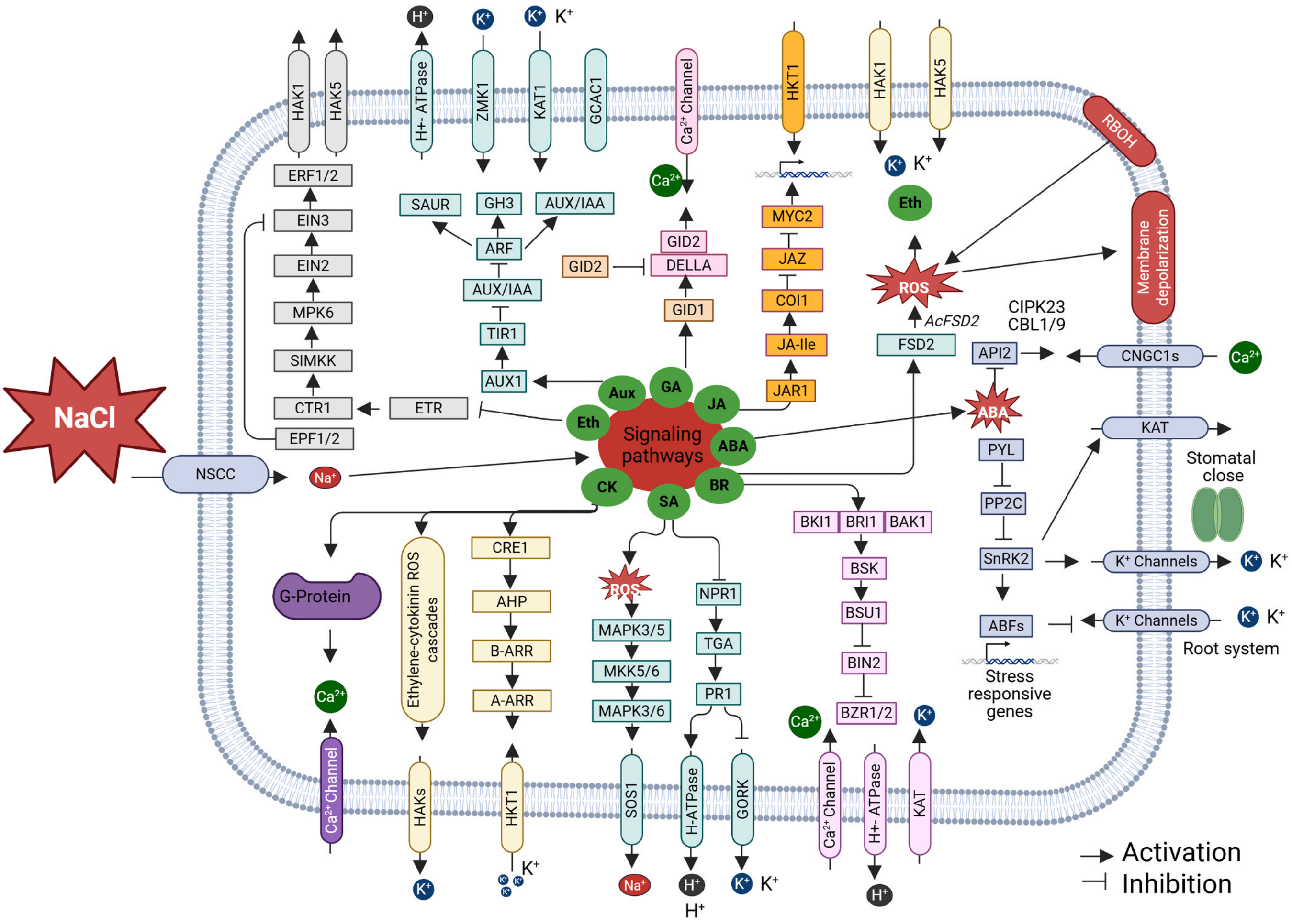

Fig. 3. The proposed model of hormonal regulation role in maintaining K^+/Na^+ homeostasis. Supplementary file 1 has the abbreviations' comprehensive meanings.

reported that auxins comprising IAA and 1-NAA can enhance cell wall elongation via participation in the activation of K^+ uptake by *Z. mays* K^+ channel 1 (ZMK1; in the cortex and epidermal cells) and stimulate H^+ pumping (Fuchs et al., 2006). Additionally, a decrease in auxin levels under abiotic stressors may result in KAT1 inactivation, which inhibits K^+ absorption (Philippar et al., 2004). Through the activation of an auxin-binding protein and the production of cytosolic pH changes, auxin has been demonstrated to be necessary for the control of guard cell anion channels (GCAC1), PM H^+-ATPase, and the activity of K^+ in/out channels. Aux and GA signaling are often linked to the regulation of Ca^{+2} influx and efflux, influencing cell division and expansion efficiency (Dindas et al., 2018; Leyser, 2018; Sakouhi et al., 2024). Small auxin-upregulated RNA (SAUR) proteins are involved in the regulations of numerous cellular, physiological, and developmental processes by activating PM H^+-ATPases and triggering cell expansions (Mohamed et al., 2022; Ren and Gray, 2015; Shalby et al., 2021).

3.2. Cytokinin (CK) and jasmonic acid (JA) signaling

CK and JA are phytohormones that play an important role in plant K^+/Na^+ homeostasis and cell morphogenesis. Shabala et al. (2009) have discovered that in the mature root zone, endogenous CKs that are produced at the root tip are transported basipetally and regulate ion fluxes. *AtARR1* and *AtARR12* (key factors in CK signal transduction) can negatively regulate the expression of *AtHKT1;1,* which is an HKT member in *A. thaliana* and is mostly found in roots to aid in keeping shoot leaf sodium levels low (Li et al., 2022b). Moreover, it was proposed that the release of dihydropyridine-like molecules and the subsequent opening of Ca^{2+} channels would result from the internalization of the CK signal by receptors attached to G proteins (Brault and Maldiney, 1999). In addition, CK is one of the components of the ethylene–CK–ROS cascade that can up-regulate high-affinity K^+ (HAK5), which improves the K^+ uptake (Nieves-Cordones et al., 2014). JA improves ion homeostasis under salt stress by reducing Na^+ uptake and increasing K^+ accumulation, which lowers the toxic Na^+/K^+ ratio in plant tissues. JA upregulates K^+ uptake transporters like HKT1 and upregulates NHX genes for Na^+ sequestration in vacuoles, leading to increased K^+ accumulation and reduced Na^+ uptake in roots. *IbNHX1/18* and *IbHKT1* ion transport-related genes have been upregulated by JA under salinity stress (Cao et al., 2016; Zhang et al., 2017).

3.3. Abscisic acid (ABA) and ethylene (Eth) signaling

ABA plays a key role in controlling ion homeostasis under salinity stress by activating stress-responsive genes and controlling the movement of ions such as K^+ into and out of cells, especially in guard cells, to enhance stomatal closure, which prevents excessive water losses under stress conditions. In maize and *A. thaliana* roots, several studies have reported that ABA can control the transport and accumulation of K^+ through activation of its channels in roots (Osakabe et al., 2014; van den Wijngaard et al., 2005). During stress, ABA-responsive TFs, like ABF1/4, can be regulated by interaction between *BnCPK4* (a member of the CPK gene family that is considered a Ca^{2+}-sensing complex) and Protein Phosphatase 2 C (PP2C) in *B. napus* (Zhang et al., 2014). Eth works to improve plant resistance to salinity by enhancing the Na^+/K^+ homeostasis, ROS, and root architecture at the right concentration. Excessive

Eth causes detrimental hyperinhibition of plant development. To provide resistance to salinity stress, Eth generated during salinity stress aids in preserving the Na^+/K^+ equilibrium (Jiang et al., 2013; Tao et al., 2015). Yang et al. (2013) have reported that compared to Col-0 (wild-type) plants, the Eth-completely or partially insensitive mutant plants (*ein2–5* or *ein3–1*) have enhanced *A. thaliana* salinity susceptibility, demonstrating how important Eth production and signaling are in controlling the salt responses of *A. thaliana* by regulating higher K^+ nutrition. Eth-releasing compounds, including the Eth precursor, 1-aminocyclopropane-1-carboxylic acid (ACC), and ethephon, can activate Ca^{2+}-permeable channels (Lang et al., 2020; Zhao et al., 2007). Conversely, a trait of NaCl resistance was observed in *A. thaliana* with a loss-of-function allele of Ethylene Overproducer 1 (ETO1), a mutant allele that results in increased synthesis of ethylene. The absence of the ETO1 role significantly improves tissue K^+ status through a mechanism unrelated to RBOHF and is linked to increased levels of HKT5 transcript (Wang et al., 2021a).

3.4. Brassinosteroids (BRs) and gibberellic acid (GA) signaling

BRs and GA are groups of plant hormones that regulate several physiological processes in salinity-stressed plants, including ion transporters and channels. Straltsova et al. (2015) have proposed that BR-activated cation-permeable channels, which are found in the PM of root cells, may play a role in the quick control of K^+ homeostasis and Ca^{2+} signaling. Exogenous application of BR can maintain ion homeostasis under salt stress in wheat (Shahbaz and Ashraf, 2007), cucumber (Nie et al., 2024), maize (Wang et al., 2024a), and kiwifruit by upregulating the expression of *AcHKT1* and the antioxidant enzyme *AcFSD2* gene (Chen et al., 2023). Moreover, Zhang et al. (2005) have found that BRs can control proton pumps and PM anion channels during *A. thaliana* cell growth. According to recent research, BR signaling is at least partially responsible for the regulation of PM H^+-ATPase (Lin et al., 2024). GA can increase the cytosolic Ca^{2+} ($[Ca^{2+}]_{cyt}$) after several hours of application and occurs via a DELLA-independent pathway, whereas GA promotes plant development by inducing DELLA degradation through the ubiquitin-proteasome pathways. It was proposed that the GA-dependent signal-transduction pathway is significantly influenced by the Ca^{2+}-ATPase gene (*OsCa-ATPase*) and its expression in rice aleurone cells (Chen et al., 1997; Okada et al., 2017).

3.5. Salicylic acid (SA) signaling

SA plays a crucial function in regulating ion homeostasis in plants, directly influencing K^+ and Na^+ transporters, channels, and protein kinases while also activating key cellular signaling pathways. In *A. thaliana*, SA enhances salt tolerance by restoring membrane potential, preventing salinity-induced K^+ leakage via the GORK channel, and reducing shoot Na^+ accumulation. SA also induced cold or heat resistance via Ca^{2+} homeostasis and antioxidant systems as reported in grape plants (Jayakannan et al., 2013). Jayakannan et al. (2015) have reported that SA restricts Na^+ influx into roots, stimulates H^+-ATPase activity, prevents root K^+ leakage, and promotes K^+ accumulation in shoots. SA also directly targets or regulates proteins involved in phosphorylation, a critical process for maintaining ion homeostasis. A key mediator is SA-induced protein kinase (SIPK), a MAPK (and ortholog of *Arabidopsis* MPK6). SIPK, often functioning alongside its close homolog MPK3, is essential for diverse stress responses in tobacco and other plants. These responses include activating the SOS1 pathway and transducing pathogen defense signals (Ding et al., 2023). Finally, under severe salt stress, SA-induced tolerance in *K. obovata* depends on NADPH oxidase-generated H_2O_2, which subsequently influences redox homeostasis and the Na^+/K^+ ratio (Wu et al., 2024).

4. Role of nanoparticles in regulating K^+/Na^+ homeostasis

Regulation of K^+/Na^+ homeostasis by NPs in plants affected by salinity stress involves a sophisticated interplay of molecular mechanisms that target signaling pathways, antioxidant systems, and ion transporters/channels. These mechanisms manage the balance in uptake, transport, and storage of ions to maintain cellular functions and overall health (Ahmed et al., 2022; Banerjee and Roychoudhury, 2022; Li et al., 2025). Several potential NPs can influence the uptake and transport of elemental ions, either beneficial (e.g., selenium (Se) and silicon (Si)) or essential elements (e.g., macronutrients including Mg, Ca, S, K, N, and P and micronutrients including Zn, Mn, Mo, Fe, Cu, B, Cl, and Ni) (Alharbi et al., 2024; Chen et al., 2020; Zhao et al., 2024). Application of NPs preserves ion balance in plants by increasing K^+ uptake, reducing K^+ efflux, reducing Na^+ uptake, and enhancing Na^+ exclusion to preserve the K^+/Na^+ level in salinity-stressed plants. These balance regulations can be controlled by activating K^+ transporters (including high-affinity K^+ (HAK) transporter (HKT) protein family, AKT1), Na^+/H^+ (NHX) antiporters and tonoplast H^+-ATPase. Several signaling pathways participate in these regulations, including Ca^{2+}, ROS, NO, and hormone signaling coordinated with gene transcriptional regulations.

4.1. Signaling pathways triggered by NPs for inducing K^+/Na^+ homeostasis

NPs have shown significant potential in modulating and enhancing various cellular processes, including Ca^{2+}, ROS, NO, and hormone signaling. The interaction between NPs and Ca^{2+} signaling in plants is an emerging area of research, and NPs can influence this process in several ways. NPs, particularly metal oxide NPs, can stimulate oxidative stress in plant cells, leading to increased intracellular Ca^{2+} levels, which then activate the plant's stress signaling pathways, such as those participating in the regulation of cell division and expansion (Kour et al., 2023; Li et al., 2024a; Tuteja and Mahajan, 2007). However, the mechanism by which NPs affect the flow of Ca^{2+} ions across cellular membranes in plants by altering the PM permeability, ER, or vacuolar membrane has not been investigated. Therefore, its function as a modulator of ion channels such as CNGCs or TRP (transient receptor potential) channels, which play a role in the influx and efflux of Ca^{2+} ions, requires further research. Future research should focus on discovering the role of NPs in altering the activity of Ca^{2+} pumps (such as the PMCA or ATPases) or exchangers (such as the NCX) that regulate Ca^{2+} gradients within the plant cell.

In addition to the role of NPs in triggering Ca^{2+} signaling, particular metallic NPs (like AgNPs, AuNPs, and ZnO NPs) were suggested to participate in inducing ROS signaling in plant cells, as discussed in several review articles (Fallah et al., 2024; Jiang et al., 2014). ROS and Ca^{2+} often engage in reciprocal regulation, where increased ROS can elevate cytosolic Ca^{2+} levels, and higher Ca^{2+} levels can further enhance ROS production, contributing to signaling cascades that regulate development, growth, and stress responses (Khan et al., 2021a; Ravi et al., 2023; You and Chan, 2015). Therefore, NPs can regulate Ca^{2+} pathways in plants by participating in the regulation of ROS signaling. However, more research is needed to support this criterion. Furthermore, it was reported that NO and hormonal signaling can also be promoted by NPs, including multi-walled carbon nanotubes (MWCNTs), to enhance the transcriptional abundance of K^+ and Na^+ transporters, maintaining the K^+/Na^+ ratio, and increasing the salt resistance of rapeseed (Zhao et al., 2019). (For more details, please refer to Sections 5 and 6.)

4.2. Role of NPs in regulating Na^+ and K^+ fluxes

Several studies have been performed to show how important NPs are in regulating K^+ absorption in stressed environments, but understanding how these NPs interact with K^+ channels remains unclear and is a promising scientific research field for the future. K^+ uptake increase and K^+ efflux reduction have been reported by application of CeO_2 and silica NPs that preserved ion balance in plant leaves under alkaline sodic soil environments (Li et al., 2022a; Liang et al., 2024; Liu et al., 2021; Rady et al., 2023; Wu et al., 2018a). Also, CeO_2 and Mn_3O_4 NPs have improved the salt tolerance in rapeseed and *Salvia leriifolia* by improving leaf K^+ retention (Khan et al., 2021b). Additionally, nano SiO_2 enhanced the levels of K^+ in the leaves, improving the growth of soybean seedlings (Farhangi-Abriz and Torabian, 2018), pea (Ismail et al., 2022), maize (Alsamadany et al., 2024), and rice plants (Alharbi et al., 2022) under salt stress. The functions of NPs in regulating K^+/Na^+ homeostasis under various levels of salinity stress conditions are presented in Table 1.

AKT, HKT and HAK ion transport members have crucial functional roles in the regulation of K^+ homeostasis under salinity stress. AKT1 is an inward-rectifying K^+ channel in *A. thaliana*, essential for root K^+ uptake. It is predominantly expressed in mature root epidermal, cortical, and endodermal cells, which is critical for its function. Mutations in AKT1 (in both *A. thaliana* and rice) severely impair K^+ absorption, leading to hypersensitivity to low-K^+ conditions (Wang et al., 2021b). In cucumber, *CsAKT1* was selected as a key gene for improving K^+ maintenance and salt tolerance by CeO_2NPs, suggesting exogenous CeO_2NPs are crucial in regulating K^+ transporters. Expression of the *AKT1* gene has been demonstrated to rise in plants when exposed to ZnO NPs, which directly improves K^+ uptake (Peng et al., 2022; Qian et al., 2024). In addition, according to reports, the *HAK5* gene was significantly up-regulated in *A. thaliana* plants treated with nano-ceria, which maintained oxidative stress, decreased depolarization of the PM potential, improved K^+ retention and decreased K^+ efflux under NaCl stress (Wu et al., 2018a). Moreover, nitrate transporter1/peptide transporter (NRT1/PTR) family (NPF) proteins play a crucial role in K^+ transport in plants, alongside nitrate (NO^{3-}) and other molecules from root to shoot, particularly in low-K^+-stressed plants. NRT1.5/NPF7.3 has function as a proton-coupled H^+/K^+ antiporter in plants to mediate K^+ translocation into the xylem and coordinate of K^+/NO^{3-} distribution (Li et al., 2017a). In tobacco (*Nicotiana tabacum* L.), carbon nanosol (CNS) treatment up-regulates the expression of *NtNPF7.3/NtNRT1.5* and has improved potassium/auxin transport, as well as antioxidant activity, metabolite levels, K^+ concentration and phytohormone profiles (Wang et al., 2024b). To confirm the role of NPs in the regulation of K^+ transporters, leaf K^+ retention, and K^+/Na^+ balance under stress conditions, tetraethylammonium chloride (TEA^+), a K^+ channel blocker, was used by Chen et al. (2020). They found that TEA^+-treated plants showed a significant decrease in K^+ accumulation, while carbon NPs (CNPs) treatment up-regulated K^+ channel expression to improve the accumulation of K^+ in BY-2 cells and ion channel protein simulation using bulk carboxyl for K^+ penetration.

Downregulation of K^+ efflux channels is another mechanism involved in the regulation of K^+/Na^+ homeostasis and cell expansion in the salinity-stressed plants treated by NPs. This was observed in cotton plants treated by CeO_2 NPs that down-regulated K^+ efflux channels (KOR) and reduced K^+ efflux under salt stress (Liu et al., 2021). In tobacco seedlings, Zhao et al. (2024) also reported downregulation of the K^+ outflow channel genes and upregulation of the K^+ influx channel gene by treatment with CNPs, which improved the absorption capacity of K^+ and plant tolerance to low-K^+.

NPs can play a multifaceted role in enhancing Na^+ exclusion and reducing Na^+ uptake in plant cells, as reported in several published studies. For example, Se-NPs can activate NHX antiporters and tonoplast H^+-ATPase and help plants compartmentalize excess Na^+ to expel it from the cell or vacuole of barley plants (Thabet and Alqudah, 2023). Intracellular NHX antiporter members have crucial functional roles in the regulation of cellular pH levels and K^+, Na^+ homeostasis by facilitating the electroneutral exchange of Na^+ and/or K^+ for protons (H^+) in plants. They utilize the H^+ gradients created by PM H^+-ATPases, as well as vacuolar H^+-ATPases and H^+-PPases, to drive either the efflux of Na^+ or K^+ out of the cell or their sequestration into vacuoles and other intracellular compartments (Ali et al., 2021).

In the salt-stressed rice and maize plants, chitosan NPs (CSNPs) and rice straw-based Si NPs have shown an upward trend in the expression of *HKT1*, *NHX1*, *Δ1-pyrroline-5-carboxylate synthetase* (*P5CS1*), *E3 ubiquitin-protein ligase*, and *plasma membrane proteolipid 3* (*PMP3*), which confers salinity tolerance by increasing K^+ and Ca^{2+} and decreasing Na^+ content (Ijaz et al., 2023; Moosavi et al., 2024). Moreover, the relative expression of *BnaNHX1* and *BnaHKT1* genes was higher in PNC-treated seedlings than in PMO, while the *BnaSOS1* gene expression level was down-regulated in PNC-treated seedlings and up-regulated in PMO-treated plants (Li et al., 2022a; Liu et al., 2021; Wu and Li, 2019).

5. Hormonal regulation by nanoparticles for improving K^+/Na^+ homeostasis

NPs modulate phyto-hormone signaling by influencing biosynthetic and catabolic pathways, altering endogenous hormone pools, and regulating the expression of hormone receptors, secondary messengers, and transcriptional regulators involved in stress response (Kumar et al., 2024a; Tripathi et al., 2022; Zhao et al., 2024). These impacts set off other signaling cascades that eventually rewire gene expression, which in turn re-regulate the activity of transporters and ion channels. Although NPs and growth phytohormones have been shown to interact in several studies, a thorough grasp of the underlying process is still mostly unknown, especially for regulating K^+/Na^+ homeostasis. NPs can affect plant hormonal signaling by interacting with plant hormones like Aux, CK, ABA, GA, and Eth; however, the proper mechanism of crosstalk between the synthesis and signaling of plant hormones and NP application is still in its infancy (Tripathi et al., 2022). Mukarram et al. (2022) have demonstrated that SiNP applications can modulate the levels of endogenous phytohormones, including JA, GAs, Eth, CKs, IAAs, and ABA, affecting the responses of various organs and tissues to stress conditions. Application of NPs to plants results in transcriptional alterations of auxin response or auxin repressor genes, ABA biosynthesis genes, Eth signaling components, and other plant hormone genes (Khalid et al., 2025). The role of ZnO NPs in the regulation of salinity stress tolerance was also reported via its role in the regulation of zeatin (ZT), gibberellin3 (GA3), auxin (IAA), which participated in down-regulating the expression of K^+ transporter genes including *MdNHX4* and *MdSKOR* (STELAR K^+ outward rectifier) and upregulating Na^+ transporter genes including *MdSOS1, MdALT1, MdCAX5*, and *MdCHX15*. This regulation improved the K^+/Na^+ ratio in seedlings of apple rootstock M9-T337 under saline-alkali stress conditions (Zhai et al., 2025). According to Gui et al. (2015), the concentrations of ABA and IAA in the roots of both non-transgenic and transgenic *Oryza sativa* plants increased in response to Fe_2O_3 NPs, suggesting that it significantly influenced the production of phytohormones. Additionally, in ginger, IAA, TZR, IP, and GA_3 levels significantly increased as a result of SiNPs treatment, which also up-regulated the expression of the genes *DELLA, AUX1*, and *B-ARR*. In addition, it was reported that AgNPs-primed seeds induced upregulation of the auxin-responsive SAUR gene, gibberellin receptor and ethylene-responsive TF (Chen et al., 2025).

5.1. Auxin (Aux)

Auxins such as IAA regulate root architecture, which is essential for efficient nutrient and ion uptake. For example, Jan et al. (2024) have shown that auxin signaling acts as an internal regulator for root growth from early organogenesis to root hair formation. According to recent reports, exposure to NPs can control plant development via influencing the biosynthesis and distribution of auxin in plants. However, the molecular mechanism regulating the role of NPs in maintaining K^+/Na^+ by auxin signaling is still unclear. TiO_2NPs have been reported to increase the auxin accumulation, auxin transport/biosynthesis genes, and PIN2 accumulation, promoting root development and elongation in

Table 1

Role of nanoparticles in regulating K^+/Na^+ homeostasis in various stressed plants.

Crop	Nanoparticleapplication anddoses	Applicationmethod	Salinity stresslevel	Effect of NPs on K^+/Na^+ Homeostasis	Refs.
Wheat (*Triticum aestivum* L.)	Fe NPs (15 and 25 mg kg^{-1} Soil)	Soil drenching	Salinity stress 6 dS m^{-1}	Fe NPs increased potassium ions (K^+) and other nutrients.	(Zia-ur-Rehman et al., 2023)
	Silver nanoparticle (AgNP)	In the nutrient solution	Salinity stress (100 mM NaCl)	AgNP improved K^+ uptake.	(Wahid et al., 2020)
	Selenium NPs (30 ppm Se-NPs)	Foliar application	Salinity stress (3000 ppm saline water NaCl)	Se-NPs up-regulated *ATPase* and *SOS1*.	(Soliman et al., 2023)
	Au NPs 300 ppm	Foliar application	Salinity stress (100 mM NaCl)	Au NPs improved the K^+/Na^+ ratio	(Wahid et al., 2022)
	Zinc oxide NPs (ZnO-NPs) 20, 50, and 80 mg L^{-1}	Foliar application	Salinity stress (6.3 dS m^{-1})	ZnO NPs increased K^+ and Ca^{2+}.	(Lalarukh et al., 2022)
Wheat and rice (*Oryza sativa* L.)	ZnO-NPs 10 mg kg^{-1} Soil	Soil supplementation	Salinity stress (7 dS m^{-1})	ZnO NPs increased the K^+/Na^+ ratio and decreased Na^+ content.	(Mazhar et al., 2023)
Rice (*O. sativa* L.)	Nano-Si	Foliar spray	Soil salinity stress (7.36 dS m^{-1})	SiNPs showed better maintenance in the K+ /Na+ Ratio.	(Alharbi et al., 2022)
	ZnO NPs 50 mg L^{-1}	Nutrient medium	60, 80, and 100 mM NaCl	ZnO NPs decreased Na^+ and increased K^+.	(Singh et al., 2022)
	Silicon (Si) NPs 20 mg L^{-1}	Foliar application	100 mM NaCl	Si NPs increased K^+ and Ca^{2+} while decreasing Na^+.	(Ijaz et al., 2023)
	Poly(acrylic acid) coated CeO_2 NPs 10 μM, 0.98 mg L^{-1}	Foliar application	Salt stress 7.2 dS m^{-1}	PNC NPs increased K^+.	(Zhou et al., 2021)
Maize (*Z. mays* L.)	Si NPs at 1.5 mM (42.1 mg L^{-1}) and 3 mM (84.2 mg L^{-1}	Seed priming	Salt stress 75 mM of Na_2CO_3	SiNPs improved K^+ uptake and translocation.	(Alsamadany et al., 2024)
	Chitosan NPs (CSNPs; 50 and 100 mg l^{-1})		Salinity Stress (NaCl of 0.07 and 0.14 g kg^{-1} soil).	CSNPs up-regulated the *high-affinity* K^+ *transporter* (*HKT1*) gene and the Na^+/H^+ *exchangers* (*NHX1*).	(Moosavi et al., 2024)
Cotton (*Gossypium hirsutum* L.)	Zinc oxide nanoparticle (ZnO NP) at concentrations of 50, 100, 150, and 200 mg L^{-1}	Foliar spray	Salinity stress (150 mM NaCl)	ZnO NPs induced the expression of *HAK17*, *AHA3*, *NHX2*, *CNGC*, and other genes, reduced *SKOR* (STELAR K^+ outward rectifier) expression, combined with the CBL-CIPK pathway, and reduced the loss of excessive K^+ and stabilized Na^+/K^+ ratio, which lessened the harmful effects of too much sodium.	(Qian et al., 2024)
	Poly acrylic acid-coated nanoceria (20 μL of PNC (0.45 mM))	Foliar application	Salinity stress (200 mM NaCl)	PNC showed lower cytosolic Na^+ (decrease up to 77 %) and higher cytosolic K^+ (increase up to 84 %)	(Liu et al., 2021)
	CeO_2 (500 mg L^{-1})	Seed Priming	Salinity stress (200 mM NaCl)	CeO_2 NPs improved Ca^{2+} and K^+ content.	(An et al., 2020)
Tobacco seedling (*Nicotiana tabacum* L.)	Carbon NPs (CNPs) at 10 mg·L^{-1}	In the nutrient solution	No stress	CNPs increased K^+ uptake through the regulation of K^+ *flux* and *ion channel* gene expression.	(Chen et al., 2020; Zhao et al., 2024)
Rapeseed *(Brassica napus)*	Polyacrylic acid-coated nanoceria (PNC)	Seed priming	Salt stress (200 mM NaCl)	PNC enhanced salt tolerance in rapeseed by modulating ROS homeostasis and α-amylase activities	(Khan et al., 2021a)
	Cerium oxide NPs (500 mg kg^{-1})	Soil supplementation	Salt stress (50 mM NaCl)	It led to Na^+ distribution in *Brassica* modification of root apoplastic barriers	(Rossi et al., 2017)
Cucumber (*Cucumis sativus* L.)	0.1 mM poly (acrylic) acid-coated nanoceria (PNC)	Foliar spray	Salt stress 75 mM NaCl	PNC showed a better-maintained K^+/Na^+ ratio.	(Peng et al., 2022)
Tomato (*Solanum lycopersicum* L.)	Copper NPs (250 mg L^{-1})	Foliar application	Salt stress (50 mM NaCl)	Cu NPs improved the Na^+/K^+ ratio	(Pérez-Labrada et al., 2019)
Ajowan (*Trachyspermum ammi* L.)	SA+nano-Fe_2O_3	Foliar application	Salinity stress (0.0, 4.0, 8.0, 12.0 dS m^{-1} NaCl	Fe_2O_3 NPs decreased salinity stress toxicity by promoting K^+ uptake and the K^+/Na^+ ratio.	(Abdoli et al., 2020)
Paper (*Capsicum annuum*)	MnNPs (0.1, 0.5, 1 mg/L).	Seed priming	100 mM NaCl	Mn NPs increased in K^+ concentration,	(Ye et al., 2020)
Pearl millet (*Pennisetum glaucum*)	AgNPs (0, 10, 20 and 30 mM)	Seed priming	Salinity (0, 120, 150 mM NaCl)	Ag NPs maintained the ionic balance of ions in plant cells (K^+, Na^+, and Na^+/K^+ ratio)	(Khan et al., 2021c; Khan et al., 2020)
Soybean (*Glycine max* L. cv. M7)	Nano-silicon (2 mM)	Foliar application	Salinity stress	Si NPs increased in K^+ concentration and decreased in Na^+ concentration.	(Farhangi-Abriz and Torabian, 2018)
Bean *(Vicia faba* L.)	ZnO NPs 50 and 100 mg L^{-1}	Foliar application	Salinity stress (150 mM NaCl)	ZnO NPs decreased Na^+ and increased K^+.	(Mogazy and Hanafy, 2022)
Arabidopsis (*A. thaliana* L.)	Poly (acrylic acid) coated CeO_2 NPs.	Leaf infiltration through a syringe	Salinity stress (100 mM NaCl)	PNC increased K^+.	(Wu et al., 2018a)
Potato (*S. tuberosum* L.)	SiO_2 NPs 1000 mg L^{-1}	Foliar application	Salt stress (0.5, 5, 8, and 12 dS m^{-1})	SiO_2 NPs decreased the Na^+/K^+ ratio.	(Kafi et al., 2021)
Tomato (*S. lycopersicum* L.)	Ca NPs 20 mM	Soil-applied	Salinity stress (50, 100, and 200 mM NaCl)	Ca NPs decreased Na^+ and increased K^+, Ca^{2+} and Mg^{2+}.	(Abeed et al., 2023)
Strawberry (Fragaria ananassa)	Se NPs (10 and 100 μM)	Foliar application	Salt stress (5 dS m^{-1}).	Se NPs applications reduced Na^+ stress and improved K^+ and Ca^{2+}.	(Soleymanzadeh et al., 2020)

A. thaliana (Wei et al., 2020). Also, Tiwari et al. (2016) have demonstrated that auxin has an important role in determining the AuNPs-induced root growth and changes in root system architecture in *A. thaliana* by upregulation of auxin-responsive genes, including *SAUR6* (*small auxin up-regulated RNA6*), *ATP-binding cassette B15*, and *inositol polyphosphate 5-phosphatase11*. Abou El-Ela et al. (2022) have found that genes involved in auxin (*SAUR41*, *auxin response factor 8* and *IAA4*) and ABA signaling (*PYL5* and *PYL4*) showed upregulation by CuO NPs treatment in rice plants. ZnO NPs treatment also up-regulated the expression of genes that participated in the auxin signaling transduction pathway, including *ARP* (*auxin-responsive protein*) in *B. napus* plants (Ahmed et al., 2022). In addition, inducing differential expression of TF genes involved in ion homeostasis, such as *bHLH*, *MYB*, and *WRKY*. Tiwari et al. (2016) have indicated that auxin signaling may be essential for regulating the alterations in *Arabidopsis* root system architecture brought on by Au NPs via upregulation of *RVE1*, *RVE2*, *LHY*, and *CCA1* as auxin-responsive genes. Zhang et al. (2018) have reported that genes involved in auxin transmembrane transport (such as *auxin efflux transmembrane transporter*), *anion transport* (such as *high-affinity nitrate transporter* (*NRT*)), and *NRT* can have their transcription increased by Cu NPs that modify the root morphology of wheat. Auxin signaling F-box protein, which provides a negative feedback control in auxin signaling, was previously shown to be down-regulated in *A. thaliana* plants treated with CuO NPs. While *SLR1/IAA14, AXR2/IAA7,* and *AXR3/IAA17* expression levels were found to be overexpressed by CuO NP treatment (Wang et al., 2016). Recently, it was investigated that genes involved in K^+ channels and transporters *AKT1, HAK, SKOR, KUP6* and *CHX17* have been up-regulated following the improved level of IAA, indicating that IAA plays a crucial role in uptake and transport of K^+ under stress conditions in tobacco (Guan et al., 2025; Li et al., 2017b). Also, there is a crosstalk between the auxin transport process and K^+ transporters, such as tiny root hair1 (TRH1, which modulates the distribution of the auxin efflux protein PIN1 and influences auxin homeostasis). TRH1 encodes a K^+ transporter involved in specific K^+ transport and translocation and required for tip growth of root hairs in *A. thaliana* (Rigas et al., 2001). Thus, by modulating auxin gradients and transporter activities, NPs ultimately affect root K^+ uptake and transport under stress; however, more research investigations are required in this research area. In another way, some reports have indicated that ZnO and Ag NPs have a negative effect on IAA accumulation in the root system of *A. thaliana*, inhibited gravitropism, and down-regulated auxin receptor-related genes *AFB1/2/3/5* and *TIR1*(Sun et al., 2017; Vankova et al., 2017).

5.2. Cytokinins (CKs)

Derivatives of adenine with aromatic or isoprenoid side chains make up the class of plant hormones known as CKs. These hormones are essential for a variety of critical development and growth mechanisms in plants, including the suppression of lateral root formation, the differentiation of xylem and phloem tissues in roots, the regulations of cell division, the differentiation of photomorphogenic cells in expanding shoots and leaves, and the inhibition of leaf senescence (Schaller et al., 2014; Wu and Hill, 2021). Faridnia et al. (2024) have found that the combination treatments with CK and nano-microelements, including Zn, Fe, and Se, improved wheat growth and yield performance. Numerous studies conducted in recent years have demonstrated the modulatory significance of CK hormone in regulating numerous aspects of plant development when exposed to stressors caused by NPs or a combination of stressors (Azhar et al., 2021; Sonkar et al., 2021; Tumburu et al., 2015). In *A. thaliana*, Vankova et al. (2017) have reported that the roots exposed to 20 and 100 mg L^{-1} of ZnO NPs (mean size 30 nm) showed increases of 280 % and 590 %, respectively, in cis-zeatin, a cytokinin linked to stress responses. Also, manganese ferrite NPs (nMnFe$_2$O$_4$) have increased CK levels by 70 % while nitrogen-doped carbon dots (N-CDs) have elevated IAA by 37 % (Wang et al., 2022a). Genes linked to the CK-mediated signaling system were shown to be elevated in *Arabidopsis* when exposed to titanium dioxide (TiO$_2$NPs) and CeO$_2$NPs (Tumburu et al., 2015). In addition, Azhar et al. (2021) examined phytohormone signaling in *Arabidopsis* after exposing the plant to various metallic NPs (ZnO, SiO$_2$, and ZnO/SiO$_2$ composite NPs). They found that the accumulation of NPs in plant tissue changed the expression level of genes related to the CK signaling pathway (*ARR7/15*), indicating the significance of CK in the plant's reaction to NPs. Vinković et al. (2017) addressed the importance of cZ CKs in Ag NPs stressed-pepper plants. On the other hand, Li et al. (2023) have shown that the application of Si-NPs resulted in an increase in the stem at joints, a decrease in CK production, and a down-regulation in the *IPT* gene in wheat leaves. This suggests that wheat stem length increased as a result of Si NP exposure. Although Aux–CK signaling plays a crucial antagonistic role in regulating the root/shoot growth ratio and plant survival under stress, studies directly investigating the role of NPs in modulating this antagonism are scarce. Research into how NPs influence Aux–CK interactions represents a promising new area for understanding NP-mediated enhancement of plant stress resistance. Modulation of plant growth through Aux–CK signaling regulation by CNPs was reported by Barot et al., (2024). Also, Vinković et al., (2017) have found that the enhanced CK level by Ag NPs at (0.01–0.1 mg L^{-1}) decreased root growth in pepper plants. Yttrium oxide (Y$_2$O$_3$) NPs inhibit *Arabidopsis* root development by disrupting polar auxin transport in the columella stem cells and quiescent center cells (Narang et al., 2025).

5.3. Abscisic acid (ABA) and ethylene (Eth)

ABA and Eth are pivotal in mediating plant responses to salinity by inducing stomatal closure, activating stress-responsive genes, and regulating ion transporters. It is also known to be involved in maintaining ion homeostasis during stress responses, and its role becomes even more significant when plants are exposed to NPs. Certain NPs can enhance ABA biosynthesis or mimic its action, leading to improved stress tolerance. Certain metal-based NPs (such as Ag, Cu, iron (Fe) and ZnO NPs) can modulate ABA levels under stress conditions, triggering the ABA-mediated signaling pathway (Fatima et al., 2023; Gui et al., 2015; Hussain et al., 2024; Wahid et al., 2020). In wheat plants, it was reported that Ag-NPs can regulate ion homeostasis through changes in ABA concentration and activate the defense systems (Wahid et al., 2020). In the treatment of *Solanum lycopersicum* L. with both Ag and Si NPs under osmotic stress, differential expression was observed in genes related to the ABA signaling pathway (Al-Khayri et al., 2023). According to Kumar et al. (2024b), exposure of rice seedlings to CNPs has strengthened relative water content and water use efficiency by regulating the ABA pathway and aquaporin genes. They have reported an increase in the expression of ABA biosynthesis genes that was verified by *AtNCED3*, *AtNCED6*, and *OsNCED1*, and downregulation of negative regulators of the ABA pathway that confirmed the increase in ABA synthesis. CNPs-induced alternation in the ABA pathway up-regulated expression of aquaporin genes (*OsPIP2–5* and *OsPIP1–3*) and modulated stomatal responses participated in improving yield quality and stress tolerance. Moreover, ABA-related genes, including the ABA sensor system such as *SNRK2s* kinases, *PP2C52, PYL4*, *PYL6*, and *ABA-biosynthesis* genes, were up-regulated in TiNPs-treated plants and enhanced resistance to osmotic stress, low phosphate and pathogen infections in *A. thaliana* (Pérez-Zavala et al., 2022). The crosstalk between ABA and Ag NPs revealed that Ag-NP and ABA were promotive to interact with AP2/ERF and offered stress recovery and submergence tolerance (Saha et al., 2021). On the other hand, the role of NPs in lowering the levels of the endogenous stress hormones, i.e., ABA and Eth, in the plant tissue was reported using AgNPs in rice (Manickavasagam et al., 2019). SiNP treatment also inhibited the production of endogenous ABA by down-regulating the expression of PP2C and B-ARR, which in turn promoted ginger rhizome germination (Zhu et al., 2025).

5.4. Gibberellin (GA)

Some studies have demonstrated the influence of NP application on endogenous GA and other phytohormones such as jasmonic acid (JA) and brassinolide (BR); however, how NPs enhance the endogenous GA content in plants is not well investigated. GA controls many plant functions, including senescence, blooming, stem elongation, and seed germination (Amorim et al., 2017; Castro-Camba et al., 2022). Alginate/chitosan (ALG/CS) nanocarriers for phytohormone GA_3 showed more efficiency than chitosan/tripolyphosphate (CS/TPP) nanocarriers in the development of *Phaseolus vulgaris* leaves and the level of carotenoids (Santo Pereira et al., 2017). The role of NPs-induced GA-ABA antagonism was reported during dormancy and germination of seeds under stress conditions in some plants in recent years. For example, it was reported role of in NPs inducing the secretion of GA via SiNPs, which have crucial roles in breaking the seed dormancy and promoting seed germination and inhibiting ABA accumulation in *Z. mays* seeds (Yuvakkumar et al., 2011). Also, the role of SiNPs in activating genes involved in the GA signaling transduction pathway in tomatoes during seed germination under salinity stress conditions and downregulating the expression of genes involved in GA deactivation and ABA (Wang et al., 2024c). Moreover, the same effect was also recorded with the addition of Fe_2O_3 NPs to peanut plants, while it promoted the levels of GA4 + 7, GA3, and ZR contents (Rui et al., 2016). Wang et al. (2020) have found that CeO_2 NP (500 mg L^{-1}) treatment raised GA levels by 20 % in roots under high nitrogen stress and by 70 % in shoots and roots under low nitrogen stress, respectively. These investigations indicate that NPs have an important role in the regulation of antagonism between ABA and GA in plants under stress conditions. At the molecular level, the exogenous Si NPs treatment enhanced expression levels of GA synthesis genes (such as *GA20ox1* and *GA20ox2*), genes involved in ABA catabolism, and suppressed the expression of genes involved in GA deactivation (such as *GA2ox1*, *GA2ox2*, *NCED1*, *NCED2*, and *AAO3*) in salt stressed-tomato seeds at the germination stage (Wang et al., 2024c). In addition, Kumar et al. (2018) examined how CNPs affected the *Arabidopsis* blooming and photomorphogenesis process by upregulating a repressor gene of the GA pathway, *RGA1* (*REPRESSOR OF GIBBERELLIC ACID 1*), by 1.7 times. They conclude that the early blooming in *Arabidopsis* is probably GA-independent.

5.5. Jasmonic acid (JA) and brassinosteroid (BR)

Jasmonic acid is a hormone signaling molecule that plays significant roles in Na^+ homeostasis and leaf senescence within halophytic plants under salinity stress. Under low levels of some NPs, JA is found to be highly accumulated and improves Na^+ homeostasis and salinity stress tolerance, for example, FeNPs have shown activation in JA-mediated defensive responses in watermelon seedlings (Kasote et al., 2019). Also, the expression of JA-related genes is up-regulated by CuNPs and chitosan-polyvinyl alcohol hydrogels (Cs-PVA) in tomatoes under salinity stress (Hernández-Hernández et al., 2018). However, the JA pathway disruption by some NPs is also reported in several studies, especially under high levels, including CuONPs and ZnONPs (Soria et al., 2019). Also, the alternation in the endogenous levels of BRs is reported by some NPs, including CeO_2 NPs and CNTs in *P. vulgaris* and *O. sativa* in recent years (Hao et al., 2016; Salehi et al., 2019).

5.6. Salicylic acid (SA)

The specific role of SA in enhancing plant resistance to abiotic stress through SA-mediated regulation of key plant metabolic pathways has come to light more and more. However, the proper mechanism of crosstalk between SA synthesis and signaling and the application of NPs to plants is still in its infancy. It was reported that Se NPs can improve the level of SA under salt stress in strawberry plants and improve antioxidant machinery and photosynthetic performance (Soleymanzadeh et al., 2020). Polyakov et al. (2023) have summarized the mechanisms of using various NP-based delivery systems for SA-controlled release to enhance stress resistance in plants. A combination of exogenous treatment with SA with several NPs, including Fe NPs to the strawberry (Dedejani et al., 2021; Mozafari et al., 2018), chitosan NPs to maize (Ma et al., 2019), chitosan NPs to wheat plants (Kadam et al., 2021), CeO_2 NPs to *Portulaca oleracea* (Hassanpouraghdam et al., 2022), and ZnO NPs to *Oryza sativa* (Faizan et al., 2021), to improve the stress tolerance and plant growth or development. In salt-stressed rapeseed, Khan et al. (2022) have found that PNC priming can promote the expression of genes linked to SA endogenous and raise the SA level in the root (78 %) and shoot (51 %) when compared to the non-nano priming group.

6. Role of Ca^{2+} signaling induced by NPs for improving K^+/Na^+ homeostasis

NPs, especially metal NPs like gold (Ag), have been shown to trigger Ca^{2+} signaling by interacting with plant cells in ways that trigger changes in intracellular levels of Ca^{2+} and affect ion channel functions (Qi et al., 2022; Yin et al., 2019). Although several research and review articles have discussed how NPs regulate Ca^{2+} signaling, the regulatory role of NPs in K^+/Na^+ homeostasis under salinity stress lacks in-depth discussion. Therefore, this review aims to elucidate the crosstalk regulatory networks governing K^+/Na^+ homeostasis under these conditions. However, the mechanism by which NPs interact with plant cells to activate Ca^{2+} signaling and regulate K^+/Na^+ flux dynamics requires further research. NPs can induce Ca^{2+} signaling in plants through a variety of mechanisms, primarily by directly interacting with membrane ion channels or indirectly by generating ROS and activating calcium-dependent signaling pathways (Germande et al., 2022; Hussan et al., 2024). The suggested role of NPs in maintaining ion homeostasis via Ca^{2+} signaling is presented in Fig. 4.

6.1. Role of NPS in directly triggering cytosolic Ca^{2+} signaling

NPs can upregulate the ion channels like CNGCs (including *CNGC1/2/4/9/13/20*), which are involved in Ca^{2+} influx via direct interaction. Activation of these channels leads to an increase in cytosolic Ca^{2+}, which further activates downstream calcium-dependent pathways, including those controlling gene expression and ion transport (Li et al., 2022c; Qian et al., 2024). The improvement in the levels of Ca^{2+} ions has increased by plant supplementation with Ca NPs, altering several physiological signaling mechanisms that may be crucial for plants' ability to adapt to stress. This increase in intracellular Ca^{2+} levels can activate the SOS (Salt Overly Sensitive) pathway that control the activity of Na^+/H^+ antiporters and helps plants compartmentalize excess Na^+ into vacuoles or expel it from the cell, thus maintaining Na^+/Ca^{2+} homeostasis (Ayyaz et al., 2022; Hussan et al., 2024; Rasheed et al., 2024; Singh et al., 2023). In the SOS pathway (the most important signaling pathway in plant salinity stress tolerance), Ca^{2+} ions can induce activation of SOS3 protein and then activate SOS2 (a serine/threonine protein kinase), and finally SOS2-SOS3 complex can activate SOS1 (a PM-localized Na^+/H^+ antiporter) to mediate Na^+ ionic transport under the high level of salt stress (Ali et al., 2023). One of the mechanisms related to the role of NPs in improving ion homeostasis by the SOS pathway is their role in regulating transcriptional levels of genes encoded in the SOS pathway. Upregulation of SOS-encoded genes was reported using several NPs, including selenium-chitosan NPs in bitter melon plants (Sheikhalipour et al., 2023), NO-CS NP in *A. thaliana* (Rahim et al., 2022), FeO NPs in *Eucalyptus tereticornis* by improving expression levels of *SOS1* with *HKT1* and *NHX* genes (Singh et al., 2021a), and SiO_2-NP application in *Citrus sinensis* 'Valencia' by upregulating *CsNHX1, CsSOS1, CsSOS2,* and *CsSOS3* transcripts inside the tissues of the roots (Mahmoud et al., 2022). This regulation in the SOS pathway by NPs successfully mitigates K^+/Na^+ homeostasis under salinity stress and enhances the antioxidant defence system, thus salinity

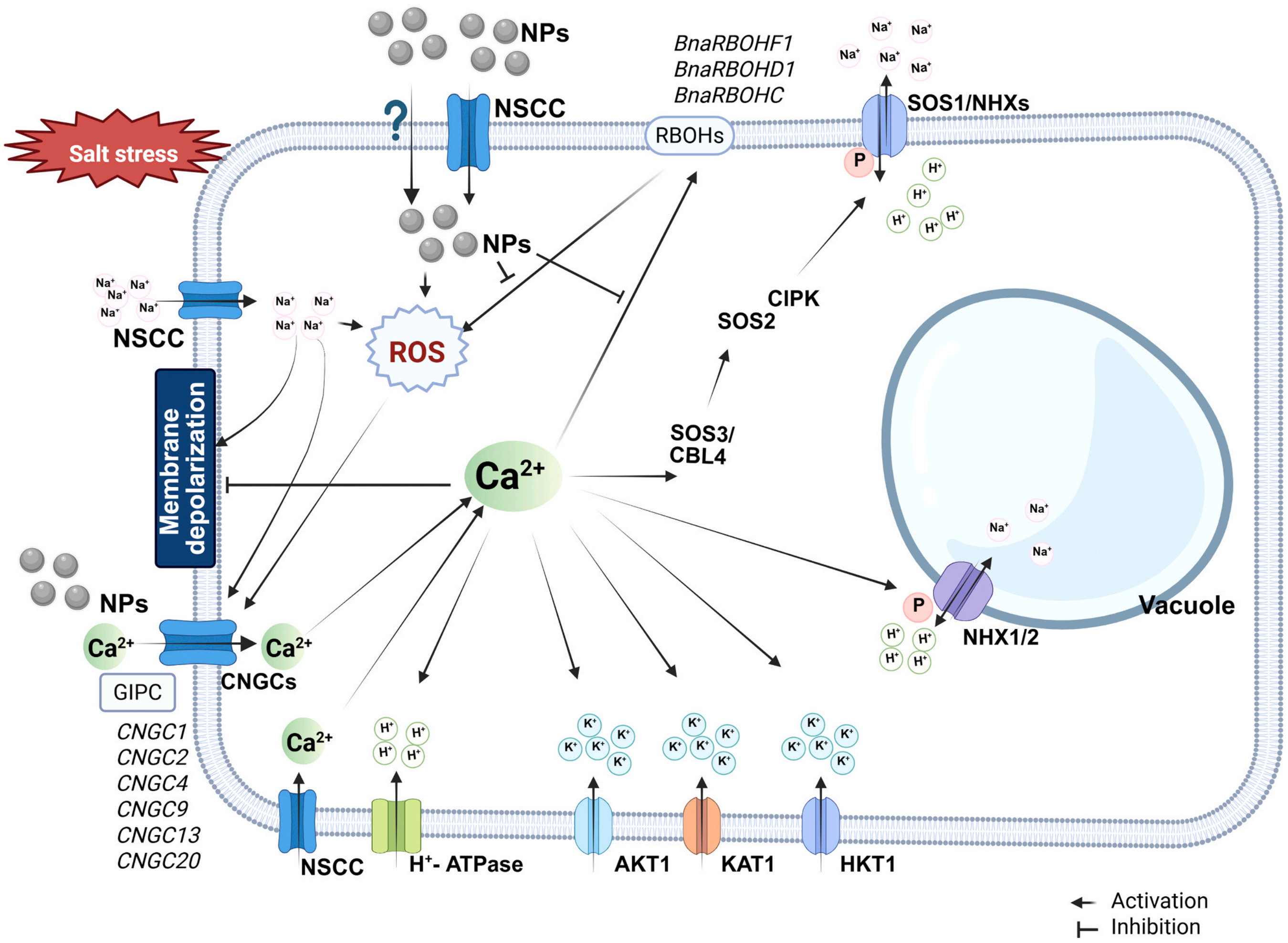

Fig. 4. A proposed model showing role of nanoparticles (NPs) in maintaining ion homeostasis via calcium (Ca^{2+}) signaling. NSCC; non-selective cation channel, RBOHs; respiratory burst oxidase homologs, SOS; salt overly sensitive, NHXs; Na^+/H^+ exchangers, ROS; reactive oxygen species, AKT1; Arabidopsis K^+ Transporter 1, KAT1; Potassium Channel K^+ channel in *Arabidopsis thaliana* 1, and HKT1; high-affinity K^+ transporter.

stress tolerance.

6.2. Role of NPs in stimulation of Ca^{2+} signaling by ROS

Stimulation of Ca^{2+} signaling by ROS induced by NPs is one of the subcellular mechanisms that were suggested to understand the role of NP application in regulating Ca^{2+} signaling in stressed plants. The generation of ROS within plant cells by application of NPs, particularly metal-based ones (e.g., Zn, Ag, CuO, nickel oxide, FeO, or TiO_2) with high concentrations, can stimulate the plant Ca^{2+} signaling pathway as reported in several published research articles (Nair and Chung, 2014; Qi et al., 2022; Soares et al., 2018). On the other hand, in *B. napus*, it was reported that SeNP application has preserved intracellular Ca^{2+} homeostasis and reduced the damage of oxidative proteins and membrane lipids by reducing the production of ROS via suppressing the expression of NADPH oxidases (*BnaRBOHF1*, *BnaRBOHD1*, and *BnaRBOHC*) and glycolate oxidase (*BnaGLO*) (Qi et al., 2021). Li et al. (2024a) reported that CeO NPs can modulate ROS and Ca^{2+} signaling that participates in promoting lateral root formation in *A. thaliana*. However, there is no research focusing on investigating the role of NPs in exploring the spatial variation of precision K^+/Na^+ regulation in various root zone specificities. In addition, the mode of action of NPs interacting with plant cells to activate Ca^{2+} signaling and control K^+/Na^+ flux dynamics remains to be further researched.

6.3. Role of NPs in activation of H^+-ATPases and K^+ transporters via Ca^{2+} signaling

Activation of K^+ transporters and H^+-ATPases is another mechanism that has also been suggested to understand the role of NP application in inducing ion homeostasis in plants via Ca^{2+} signaling. This activation mechanism was reported by NPs induced Ca^{2+} signaling that participates in the activation of H^+-ATPases and K^+ transporters, including AKT1 and KAT1. Elevated Ca^{2+} levels can promote the activation of these transporters, ensuring proper K^+ uptake and preventing K^+ deficiency under stress conditions (Kumari et al., 2021; Mishra et al., 2024; Shabala and Pottosin, 2014). Fe_2O_3 NPs have improved ATP (Adenosine triphosphate) content and H^+-pump activities that can reduce Na^+ uptake and translocation while improving the uptake of nutrients in the leaves and roots of ajowan plants (Ghassemi-Golezani and Abdoli, 2021). Moreover, a new nanotechnology that involves Ca^{2+} signaling and the SOS pathway to improve ion homeostasis and salinity tolerance based on transient gene silencing via using small interfering RNA (siRNA) delivery techniques in plants has been addressed recently. Specifically, researchers explore the use of NPs such as mesoporous silica nanoparticles (MSNs) to deliver target siRNA into plant cells, enabling efficient and targeted gene silencing into mature plant leaves. Y. Cai et al. (2024) have studied the efficacy of this delivery technology by silencing the *SOS* gene using MSN-siSOS in *Nicotiana benthamiana* leaves. Their findings revealed that successful *SOS* gene silencing significantly reduced abiotic stress resistance. This investigation suggests that this technology is a promising tool for improving ion homeostasis and addressing salinity stress tolerance by silencing key genes involved in salinity stress sensitivity. However, further research is also crucial in this regard.

7. Role of crosstalk between Ca^{2+} and hormone networks mediated by NPs in the regulation of K^+ and NO signaling

The induced Ca^{2+} and hormone signaling by NPs can participate in promoting cellular signaling pathways through their interaction with plant cell components, especially those associated with K^+/Na^+ homeostasis. For instance, the induced Ca^{2+} signaling can promote signaling molecules, including K^+ and NO, which in turn can activate or inhibit TFs that control ion transporters or channels (Banerjee and Roychoudhury, 2022; Cameron et al., 2022; A. Singh et al., 2024a). These induced signaling pathways, in turn, help to maintain the balance of ions such as K^+, Na^+, Ca^{2+}, and others. The interactions between NPs and these signaling network pathways are complicated and context-dependent, but they generally involve several key mechanisms. NPs can indirectly influence K^+ signaling in plants through several mechanisms that involve the modulation of ion channels, transporters, and TFs. Ca^{2+} signaling can involve RBOH proteins, which were reported to have a crucial role in the production of ROS signaling in stressful environments (Kumari et al., 2021; Thabet et al., 2024; Wang et al., 2023). The role of NPs mediated Ca^{2+} and ROS signaling in the regulation of K^+ signaling to maintain K^+/Na^+ homeostasis is represented in Fig. 5.

7.1. K^+ signaling

K^+ signaling is one of the key plant signaling which are critical for numerous cellular functions such as osmoregulation, enzyme activation, stomatal movement, and maintaining cell turgor pressure. Moreover, K^+ and Ca^{2+} are often coordinated in their transport, and Ca^{2+} acts as a secondary messenger in K^+ signaling (Kour et al., 2023). The induced H_2O_2 (as one of the ROS) can control K^+ signaling under abiotic stress conditions in plants. This results in a unique H_2O_2-dependent signaling pathway that improves the plant's capacity to withstand salinity stress (Fallah et al., 2024; Rai-Kalal et al., 2021). Under salt stress conditions, RBOH, a NADPH oxidase that generates ROS in apoplasts, is linked to CeO_2 nanoparticle-activated K^+ regulation. Mutants of the *OsRbohA* gene knockout exhibited lower salt resistance, lower ROS production, and an imbalance in ion homeostasis in *Oryza sativa* (Li et al., 2025; Wang et al., 2022b). The same findings have also been reported using $nSiO_2$ that regulated RBOH-mediated H_2O_2 generation and induced K^+ signaling, thus participating in adjusting the redox homeostasis in quinoa plants. Interestingly, in quinoa plants exposed to lead toxicity, exogenous SiO_2 NPs have been shown to enhance plant stress response by controlling NADPH oxidase-dependent ROS signal transduction. This suggests that NPs may enhance plant stress response by controlling NADPH response in the pathway of K^+ transporters (Karimi-Baram et al., 2024). Moreover, to control Na^+/K^+ and redox balance, the mangrove plant *Kandelia obovata* activated NADPH oxidase-dependent H_2O_2 signaling, which increased K^+ inflow under saline conditions (Wu et al., 2024). Conclusively, excessive K^+ loss under high salt stress from the cells led to ionic imbalance through signaling pathways related to ROS- and Ca^{2+}-activated GORK channels or K^+ channels thus reducing K^+ retention. In contrast, NPs application has a significant role in the activation of K^+ signaling through crosstalk with Ca^{2+} signaling and RBOH-mediated ROS signaling, suggesting that NPs improve plant stress responses by controlling NADPH function. In addition, NPs play a crucial function in ionic homeostasis by regulating transcriptional levels of K^+ channels and transporters' genes, including *KAT1* and *HAK5*.

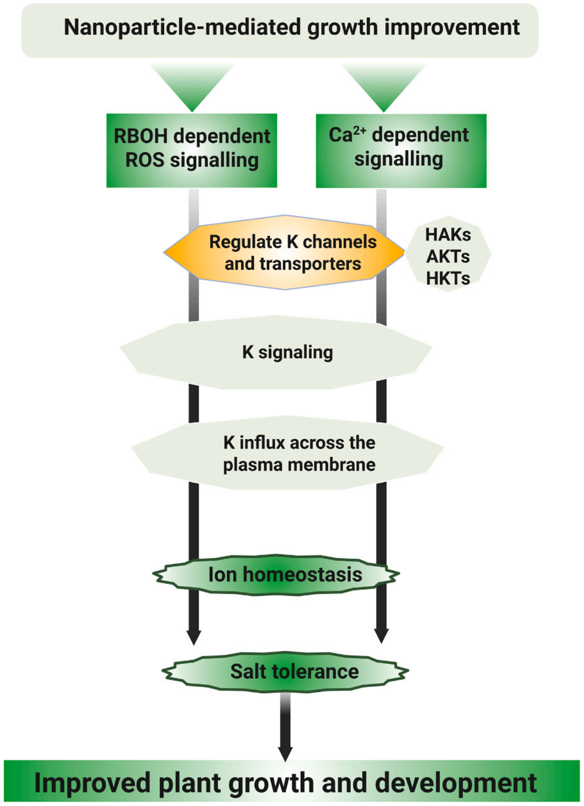

Fig. 5. Role of nanoparticles mediated calcium (Ca^{2+}) and reactive oxygen species (ROS) signaling in the regulation of potassium (K^+) signaling to maintain ion homeostasis (particularly K^+/Na^+ homeostasis) and salinity stress tolerance.

7.2. NO signaling

It was reported that Ca^{2+} fluxes participate in NO production; however, some studies have highlighted that NO is one of the key messengers mediating Ca^{2+} signaling. Under stress conditions, NO can be produced as a secondary free radical from the metabolic processes, and it can induce an influx of Ca^{2+} under stress conditions (Jeandroz et al., 2013; Seifikalhor et al., 2019). In addition, *AtCaM3* (Calmodulin 3 (*CaM3*)) participates in NO signaling as a downstream factor. Induced Ca^{2+} signaling has been shown to activate nitric oxide synthase (NOS) through CaM and/or CaM-like protein (CML) (Ma et al., 2008; Xuan et al., 2010). The NO/Ca^{2+} pathways may affect many cellular functions, such as auxin-mediated adventitious root formation as well as ABA-promoted stomata closure (Astier et al., 2010).

NPs application was reported to be involved in enhancing NO production in plant cells by increasing a crucial signaling molecule, raising plant hormone levels, controlling gene expressions, preserving ion homeostasis and nutrient absorption, lowering levels of ROS via scavenging or antioxidant defence system activation, and enhancing photosynthesis efficiency; therefore, NPs can assist plants in overcoming salinity stress (Chen et al., 2015; Kolbert et al., 2021; Silveira et al., 2019b). The role of the crosstalk between Ca^{2+} and plant hormones signaling networks mediated by NPs in the regulation of $NO^{\cdot}$ signaling and ion channels which enhance K^+/Na^+ homoeostasis are represented in Fig. 6. Soni et al., (Soni et al., 2024) and Fu et al., (Fu et al., 2023) have discussed the mechanisms of NP role in mitigation the NO signaling as a signaling molecule to control many metabolic processes in plants, however, further investigation is required to have a deeper comprehension of the crosstalk between Ca^{2+} and phytohormone signaling induced by NP application and NO signaling pathway to design suitable NPs to improve plants' ability to withstand stress. The impact of several nanoparticles (namely CS NPs (Ma et al., 2019; Methela et al., 2023), metal oxide (MO) NPs (Ahmad et al., 2022), and carbon nanotubes

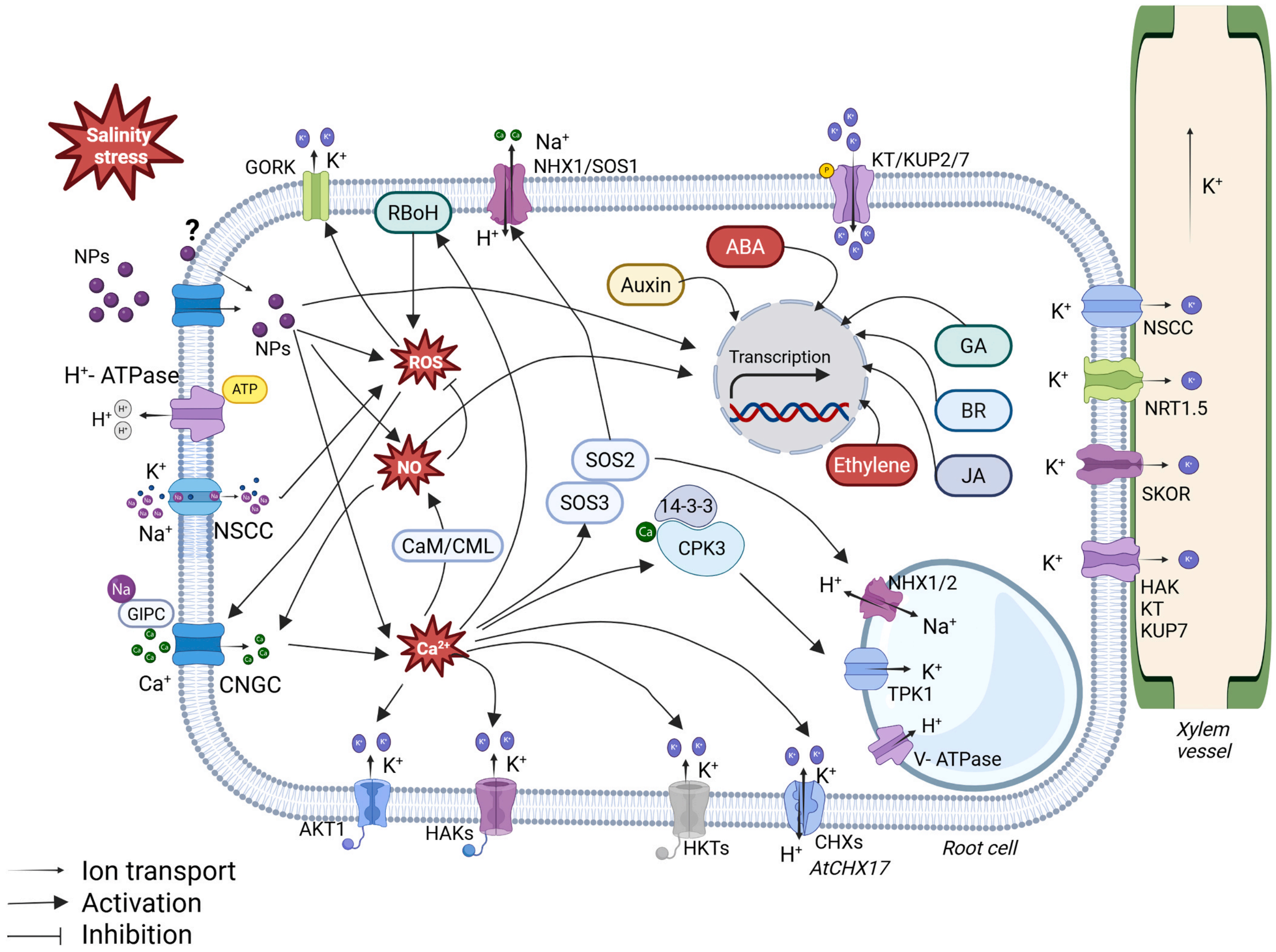

Fig. 6. Role of the crosstalk between Ca^{2+} and plant hormones signaling networks mediated by nanoparticles (NPs) in the regulation of K^+ and NO signaling, which regulate K^+/Na^+ homeostasis. NPs; nanoparticles, GORK; guard cell outward-rectifying potassium efflux channels, SOS1; salt overly sensitive 1, NHX1/2; Na^+/H^+ exchanger1/2, CNGC, cyclic nucleotide-gated channels, RBOH; respiratory burst oxidase homologous, V-ATPase; vacuolar ATPase, H^+-ATPase; plasma membrane H^+-ATPase, AKT1; inward-rectifying K^+, HAKs; High Affinity K^+ transporters, CHXs; HKT; high-affinity K^+ transporters, GIPC; glycosyl inositol phosphorylceramide, NSCC; non-selective cation channels, ATP; Adenosine triphosphate, NRT1.5; high-affinity nitrate transporter1.5; SKOR; STELAR K^+ outward rectifier, ROS; reactive oxygen species, and NO; nitric oxide.

(CNTs) (Zhao et al., 2020b; Zhao et al., 2019) on endogenous NO production and signaling in various plant species has been reported by several papers.

Some NPs, like those loaded with NO-releasing compounds (e.g., S-nitroso-N-acetylpenicillamine (SNAP) or sodium nitroprusside (SNP)), can serve as NO donors, directly releasing NO into plant tissues (Pelegrino et al., 2021; Seabra et al., 2014; Silveira et al., 2019a). This provides a controlled and sustained source of NO for plant signaling processes. The mechanisms behind the NO production brought on by poly (acrylic acid) coated nanoceria (PNC) treatment were further clarified by Zhou et al. (2021). According to this study, PNC promoted *nia2* gene transcription (nitrate reductase is encoded by this gene) and aided in its protein dephosphorylation, which led to *nia2*-dependent NO production. NO function in lowering ROS buildup and preserving ion homeostasis has been used to explain how NP-mediated NO induces salinity tolerance in rice plants. NO-releasing NPs; NO donor S-nitroso-mercaptosuccinic acid (S-nitroso-MSA) encapsulated in chitosan NPs (CS NPs) has increased NO bioactivity in *Z. maize* plants under salinity stress (Oliveira et al., 2016). This novel technique of NO-releasing is a promising technology to overcome heavy metal-contaminated soil or irrigation water to decrease their toxicities in plants (Pande et al., 2022). For example, NO-releasing chitosan NPs have improved nutritional balance in soybean plants and enhanced photosynthetic maintenance under copper stress (Gomes et al., 2022). The effect of NPs or NO-releasing NPs in regulating NO levels in plants and their role under different environmental conditions are presented in Table 2. In general, Seabra et al. (2022) have mentioned that the progress of using NO-releasing nanomaterials in plant science is not enough, and it needs more research to understand the mode of action in plants and how to deliver this technology to be applied in the field at a large scale.

8. Role of Ca^{2+} and hormone signaling mediated by NPs in the regulation of TFs related to K^+/Na^+ homeostasis

8.1. *Transcription factors (TFs) and K^+/Na^+ homeostasis*

TFs are essential for controlling K^+/Na^+ homeostasis that involves modulating the gene expressions that control ion transporters, channels, and pumps in the PM, vacuole, and other intracellular membranes, in addition to genes involved in ion sensing and signaling pathways (Amin et al., 2021; Du et al., 2023). These transporters control the uptake, distribution, and sequestration of ions such as K^+, Ca^{2+}, Na^+, Cl^-, and others (Li et al., 2024a; Wu, 2018). *Sensitive to Proton Rhizotoxicity1* (*STOP1*) TF can control K^+ uptake and distribution by modulating K^+

Table 2
Effect of nanoparticles (NPs) or nitric oxide (NO)-releasing NPs in regulating NO levels in plants and their role under stress conditions.

Nanoparticles (NPs)	Plant Species	Role	Refs.
Multi-walled carbon nanotubes (MWCNTs)	*Arabidopsis thaliana* L. and *Brassica napus* L.	MWCNTs regulate genes involved in the development of root hair, and ethylene could participate in this pathway after NO.	(Zhao et al., 2020b)
Poly (acrylic acid) coated cerium oxide NPs (PNC) (1 μM, 98 μg L^{-1})	Rice seedlings	enhanced NO production and decreased ROS accumulation.	(Zhou et al., 2021)
MWCNTs	*Brassica napus* L.	NO might act downstream of MWCNT signaling in plant tolerance against	(Zhao et al., 2019)
Chitosan NPs (CSNPs), including S-nitroso-mercaptosuccinic acid (S-nitroso-MSA), a NO donor	Maize plants (*Zea mays* L.)	S-nitroso-MSA nanoencapsulation can improve NO bioactivity under salinity stress conditions in plants.	(Oliveira et al., 2016)
Nitric oxide-releasing chitosan NPs (GSNO-CS NPs)	Sweet cherry fruit	GSNO-CS NPs improve the levels of NO, which alter ROS levels by antioxidant regulations.	(Ma et al., 2019)
Chitosan NPs containing S-nitroso-mercaptosuccinic acid (S-nitroso-MSA)	Neotropical tree (*Heliocarpus popayanensis* Kunth)	S-nitroso-MSA nanoencapsulation increased NO level, relieved oxidative stress, and improved relative water content and photosynthesis.	(do Carmo et al., 2021)
Chitosan NPs containing NO donors: *S*-nitrosoglutathione (GSNO) or *S*-nitroso-*N*-acetylcysteine (SNAC)	Sugarcane plants	SNAC or GSNO enhanced the NO levels and stress resistance in sugarcane plants.	(Silveira et al., 2021)

channel expression and can regulate gene expression involved in maintaining proton balance, particularly under acidic conditions in plant roots (Chandran et al., 2024; Li and Tian, 2023; Tokizawa et al., 2023). In response to low-K^+ stress in *A. thaliana*, *STOP1* can positively regulate *low potassium sensitive 1* (*LKS1*) transcription by interacting with the Ca^{2+}-binding (CBL1/CBL9) proteins, and phosphorylates AKT1 to improve K^+ absorption (Wang et al., 2021c). C2H2-type zinc finger proteins (ZFPs) have an important role in ion homeostasis regulations and salinity stress responses in plants. For example, the CIPK (CBL-Interacting Protein Kinases) family respond to Ca^{2+} fluctuations by activating downstream signaling pathways, helping maintain ion homeostasis. In the salt regulatory signaling pathway, ZFP182 can up-regulate downstream ion-transport-related genes, including Na^+ transporter genes and help in Na^+ excretion from the cells (Chen, 2012; Roychoudhury and Banerjee, 2017). *CpSPL5* and *CpSPL8* TFs have been reported to participate in inhibiting the SOS pathway and negatively regulate NaCl resistance in *Codonopsis pilosula* by significantly increasing the contents of Na^+ and decreasing K^+ (Li et al., 2024b). Overexpression of *FaMYB63* TF has been reported to directly bind to the SOS1 promoter and enhance NaCl resistance in *A. thaliana* (Wang et al., 2024d). Also, it was reported that under salt stress, SOS2 and SOS3 transcriptions can be induced by MAPK4-activated MYB42 TFs, whereas SOS3 expression can be suppressed by zinc-binding protein 2 (PLATZ2) and plant AT-rich sequence (Ahmed et al., 2024; Ali et al., 2023; A. K. Singh et al., 2024).

8.2. *Activation of TFs related to K^+/Na^+ homeostasis by NPs*

Several studies have suggested that NPs like TiO_2 and ZnO may activate stress-responsive TFs such as *WRKY*, which can then control the expression of genes responsible for K^+ transport under stress conditions. *WRKY* family members can be activated by various stresses; these TFs regulate the expression of genes that participate in K^+ transporters and pumps (Huang et al., 2024; Mirakhorli et al., 2021; Wagan et al., 2024). Moreover, they can influence the *SOS1* gene, which encodes a Na^+/H^+ exchanger. The activation of the *SOS2* kinase by these NPs may help maintain potassium uptake and balance under salt stress by enhancing potassium transport and reducing sodium toxicity. *DREB2A* (*Dehydration-responsive element-binding protein 2A*), *ABF* (*ABA-binding factors*), and *CAMTA* TFs modulate the expression of genes that affect ion transport and help to preserve cellular osmotic balance and Na^+/K^+ homeostasis (Altaf et al., 2021; Zaman et al., 2022). *NAC* and *bHLH* TF families contribute to regulating transporter genes that control the uptake and distribution of ion transport and nutrient homeostasis across various tissues. The identified-NAC TF (*PeNAC1*) from *Populus euphratica* was reported to maintain Na^+/K^+ homeostasis and improve salt resistance in *A. thaliana* (Li et al., 2023; Yang et al., 2018). It was reported that ZnS-T NPs can augment expression-specific TFs involved in of plant growth of *Oryza sativa* seeds and trigger the antioxidant defense network (Khepar et al., 2024). NPs can induce oxidative stress or mimic stress conditions (like salt or drought stress), triggering the activation of stress-responsive TFs such as *DREB* (*dehydration-responsive element-binding proteins*), *ABF/AREB* (*ABA-responsive element-binding factors*), and *bZIP* TFs. These TFs help regulate the expression of genes related to K^+/Na^+ homeostasis under stress conditions (Ahmed et al., 2024; Boora et al., 2024; Linh et al., 2020; Liu et al., 2023b).

Conclusively, application of NPs to the plant or soil offers a promising approach to lessen the salinity stress impact in plants by their role in inducing Ca^{2+} and hormonal signaling networks that activate key subcellular signaling cascades, including ROS, K^+, and NO signaling, altering key ion transporters and supporting antioxidant defenses. Moreover, these NPs-induced subcellular signaling maintain K^+/Na^+ balance via reducing Na^+ absorption and improving K^+ uptake (Fig. 7). This balance is managed by intricate communication between $Ca^{2+}$and hormonal signaling networks that control genes and TFs such as *bHLH*, *WRKY*, *NAC*, *MYB*, *CAMTA*, *ABF/AREB*, *bZIP*, *ERFs*, *R2R3MYB*, and *NFX1*. This complex crosstalk can activate K^+ transport proteins, including HKT1 and salt overly sensitive1 (SOS1) and other transporters (Fig. 7).

9. Nanoparticles and stomatal motion and anatomy

NPs have emerged as significant agents in plant stress tolerance because of their distinct physicochemical and anatomical characteristics, which can influence physiological processes at the molecular and cellular levels (El-Saadony et al., 2022; Rasheed et al., 2022). One such area of interest is the regulation of stomatal movement, which is mainly controlled by K^+/Na^+ homeostasis, crucial for plant water regulation, gas exchange, and overall plant homeostasis (Amir et al., 2024). Although NPs therapy significantly contributes to stomatal anatomy and regulation (Rehman et al., 2024), more investigations are required to identify the methods by which NPs control stomata movements. The function of NPs in controlling stomata through K^+/Na^+ homeostasis involves several mechanisms, including altering ROS levels, promoting Ca^{+2} signaling, influencing hormone signaling networks, regulating ion transporters, maintaining K^+/Na^+ homeostasis, and modifying the plant's stress responses (Etesami et al., 2021; A. Singh et al., 2024a).

9.1. *Role of ion homeostasis in regulating stomata motions*

Stomatal motion is primarily controlled by the closing and opening of the guard cells of stomata, which involves the active transport of ions (mainly K^+ ions) into and out of the cells (Kollist et al., 2014). The movement of these ions is controlled by ion channels and pumps, such as the H^+-ATPase pump, K^+ channels, and anion channels (Gadsby, 2009).

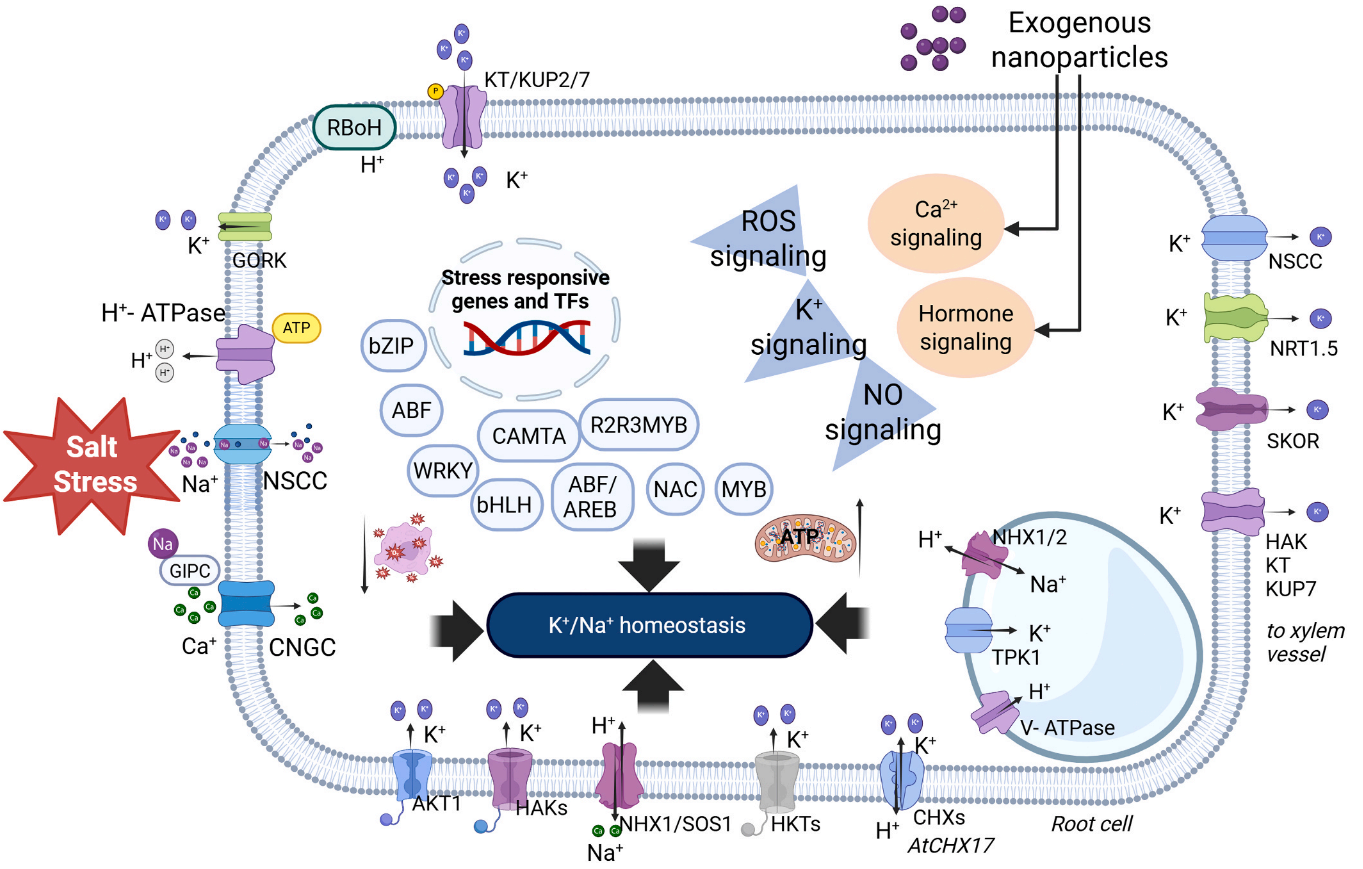

Fig. 7. The proposed model of nanoparticle functions in controlling K^{+}/Na^{+} homeostasis under salinity stress circumstances is depicted in a simplified schematic photograph. GORK; guard cell outward-rectifying potassium efflux channels, SOS1; salt overly sensitive 1, NHX1/2; Na^{+}/H^{+} exchanger1/2, CNGC, cyclic nucleotide-gated channels, RBOH; respiratory burst oxidase homologous, V-ATPase; vacuolar ATPase, H^{+}-ATPase; plasma membrane H^{+}-ATPase, AKT1; inward-rectifying K^{+}, HAKs; High Affinity K^{+} transporters, CHXs; HKT; high-affinity K^{+} transporters, GIPC; glycosyl inositol phosphorylceramide, NSCC; non-selective cation channels, ATP; Adenosine triphosphate, NRT1.5; high-affinity nitrate transporter1.5, SKOR; STELAR K^{+} outward rectifier, ROS; reactive oxygen species, and NO; nitric oxide.

In guard cells, H^{+}-ATPases are membrane proteins that pump protons (H^{+}) out of cells, creating an electrochemical gradient which drives the influx of K^{+} and other osmolytes into guard cells, increasing their turgor pressure and causing stomatal opening. H^{+}-ATPases can be activated by blue light (BL), promoting stomatal opening, while ABA inhibits this BL-induced H^{+}-ATPase activation. In addition, ABA can also directly regulate K^{+} channels, affecting K^{+} uptake and influencing stomatal responses (Tsuzuki et al., 2013; Zuo et al., 2025). Moreover, RBOH enzymes, particularly *Arabidopsis* guard cell isoforms AtRBOHD and AtRBOHF, are key ABA-regulated ROS producers essential for stomatal closure. OST1 kinase acts upstream, directly phosphorylating and activating AtRBOHF to trigger ROS production. Additionally, CBL1/CBL9-CIPK26 complexes emerge as regulators, enhancing AtRBOHF-derived ROS, linking ROS to anion channel activation signaling (Sierla et al., 2016). ROS act as signaling molecules, and their production and accumulation in guard cells can trigger a cascade of events, including changes in Ca^{2+} concentration and the activation of protein kinases, which further modulate K^{+} channel activity (Evans et al., 2016).

9.2. NPs induced stomatal ion homeostasis via ROS, Ca^{2+} and hormone signaling

According to reports, the use of certain NPs can participate in enhancing or scavenging ROS in stressed plants to promote signaling transduction effect that induces stomatal motion as a protective response under environmental conditions (Jampílek and Kráľová, 2021). Under salt and low-temperature stress, 100 mg L^{-1} SiO$_2$ NPs have improved the stomatal traits, including stomatal length, width, and density by decreasing the ROS activity and malondialdehyde level (Liang et al., 2023). The ability of NPs to decrease oxidative stress was also reported in spinach and *Linum usitatissimum* L. treated by 150 μM spinach-assisted AuNPs (S-AuNPs) and 50 mg L-1 ZnO, respectively, which improved the cytosolic Ca^{2+} and photosynthetic performance, modified the ABA content, and maintained stomatal aperture under salinity stress conditions (Amir et al., 2024; P. Singh et al., 2021b). However, another study reported that CeO$_2$ NPs increased ROS accumulation participated in the decreased stomatal conductance (Gs) and photosynthetic rate and activated the pathway of stomatal closure (Guo et al., 2024). The downregulation of ABA negative regulators and upregulation of ABA biosynthetic genes in rice and *Arabidopsis* plants by exogenous application of CNPs, with the increase in Gs and stomatal size, has confirmed the pivotal role of ABA signaling in NPs-regulated stomatal traits in plants (Kumar et al., 2024b). Also, the upregulation of *GmWRKY27* genes after NPs treatment has highlighted the correlation between signaling and synthesis of ABA and stomatal function in the stressed plants (Linh et al., 2020). It was reported that several NPs, including CNPs, can improve ion transport, such as K^{+}, through uptake and accumulation in plant cells (Chen et al., 2020). This change in the ion transport mechanism can influence turgor pressure in guard cells that are responsible for stomatal movement to be opened. Triggering high PM H^{+}-ATPase activity was reported to be another mechanism for NPs-mediated stomatal regulation by decreasing apoplastic pH, since the isoform of H^{+}-ATPase has been reported to be responsible for stomatal opening and increasing CO$_2$ uptake (Kim et al., 2015).

10. Conclusions and future perspectives

In salt-stressed plants, K^+/Na^+ homeostasis is a complex, multifaceted process that helps manage osmotic pressure, ion toxicity, and nutrient balance. Plants can lessen the detrimental effects of salinity by actively controlling the uptake, efflux, and compartmentalization of ions and maintaining cellular functions necessary for growth and survival. This ability to control ions like Na^+, K^+, and Ca^{2+} in response to salinity stress is a key mechanism of resistance to salinity stress in plants. Maintaining K^+/Na^+ balance mediated by NP application is managed by intricate communication between $Ca^{2+}$and hormonal signaling networks that activate key subcellular signaling cascades, including ROS, K^+, and NO signaling. These signaling networks control genes and TFs, such as *bHLH*, *WRKY*, *NAC*, *MYB*, *CAMTA*, *ABF/AREB*, *bZIP*, *ERFs, R2R3MYB*, and *NFX1,* that respond to stress, altering key ion transporters and supporting antioxidant defenses. Thus, NPs application can reduce Na^+ absorption and improve K^+ uptake and maintain K^+/Na^+ balance. This complex crosstalk can activate K^+ transport proteins, including HKT1 and salt overly sensitive1 (SOS1) and other transporters. However, understanding how these NPs interact with K^+ transporters and Ca^{2+} channels, such as CNGCs, remains unclear and is a promising scientific research field for the future.

New future research should also be concerned with discovering the role of NPs in altering the activity of calcium pumps (like the PMCA or ATPases) or exchangers (like the NCX) that control Ca^{2+} gradients within the plant cell. With the development of new imaging and isotope technologies, the possible role of NPs in triggering Ca^{2+} release from internal reserves, such as the ER or vacuoles, and enhancing the cytosolic Ca^{2+} concentration, can be detected in the coming research. Studies based on transient gene silencing delivery using NPs to deliver target siRNA into plant cells are a promising tool for improving K^+/Na^+ homeostasis. However, further research is crucial for addressing salinity stress tolerance by silencing key genes involved in salinity stress sensitivity. In addition, the progress of using NO-releasing nanomaterials in plant science is not enough, especially for K^+/Na^+ homeostasis, and it needs more research to understand the mode of action in plants and how to deliver this technology to be applied in the field on a large scale. Further research is required to investigate the role of NPs in the regulation of phospholipid signaling pathways under salinity stress, as several membrane phospholipid signals are produced five minutes after being exposed to osmotic stress or ionic stress. Moreover, these further studies should optimize NPs' uses, assess long-term environmental impacts, and ensure cost-effectiveness for large-scale adoption to maximize their potential application and improve the sustainability of crop production.

CRediT authorship contribution statement

Conceptualization, I.A.A.M, H.H.W., and Z.J.Y.; Formal analysis, I.A.A.M, M.B., H.H.W., and Z.J.Y. Funding acquisition, M.F.F, H.H.W., and Z.J.Y.; Investigation and Methodology, I.A.A.M, M.B., C.J.F., J.W., H.H.W., and Z.J.Y. Validation and Visualization, I.A.A.M., M.B., E.F.A.A., C.C.F., and J.W.; Supervision, Resources and Project administration, H.H.W. and Z.J.Y.; Writing – original draft, I.A.A.M., I.U.K., J.W., H.H.W., Z.J.Y.; Writing – review & editing, I.A.A.M, M.F.F., I.U.K., J.W., H.H.W., and Z.J.Y. All authors have read and agreed to the published version of the manuscript.

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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.

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Appendix A. Supporting information

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Data availability

No data was used for the research described in the article.

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