REVIEW

The Role of Phytohormones in Alleviating Salt Stress in Rice

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ABSTRACT

Rice is a crucial food crop globally. Soil salt stress has adverse effects on the physiology and biochemistry of rice, leading to ionic toxicity and disrupted metabolism. Research aimed at improving salt tolerance and understanding its underlying mechanisms in rice is becoming increasingly important. Phytohormones are crucial in managing rice's reaction to salt stress by controlling its physiological and biochemical functions. Some phytohormones can improve salt tolerance in rice by affecting gene programming, protein expression, and salt stress signaling, thereby helping rice adapt to salt-stressed environments. This review highlights recent advancements in understanding how various phytohormones—such as abscisic acid (ABA), auxin (IAA), cytokinins (CKs), jasmonates (JA), gibberellins (GAs), melatonin (MT), salicylic acid (SA), ethylene (ETHY) and brassinosteroids (BRs)—help mitigate the detrimental effects of salt stress in rice. Additionally, we explore the current challenges and future research directions for utilizing exogenous phytohormone regulators to boost rice's resistance to salt stress.

KEYWORDS

Phytohormones; salt stress; rice growth; salt tolerance

1 Introduction

Rice, known scientifically as *Oryza sativa* L., is a crucial staple food and cereal crop with global significance. In 2021, global rice production reached 787 million tons [1], making it the second most cultivated cereal crop globally. Given the growing global population, it is projected that the rice supply will need to double by 2050 to satisfy the rising demand for food [2]. However, various factors impact rice growth, including environmental stress, management strategies, and nutrient deficiencies. Among these, abiotic stress, particularly salt stress, is a major influence affecting rice development and yields worldwide [3].

The salinization of soil poses a major environmental challenge to agriculture, putting enormous pressure on agricultural production and hindering the sustainable development of agriculture [4]. On the one hand, soil salinization poses a serious threat to agroecosystem health [5] and is expected to be exacerbated by climate change, such as prolonged droughts and sea level rise [6]. On the other hand, salt stress significantly threatens crop production in irrigated lands, with an estimated one-third of the global

irrigated croplands facing this challenge [7]. It adversely affects plant growth and crop yields. The soil affected by salt can lead to nutrient deficiencies, stunted plant growth, and decreased overall productivity. For rice production, it is reported that salt stress results in a 50% reduction in global rice production [8], which has an impact on the global food supply.

In rice, salt stress induces physicochemical changes in grain composition and quality [9] and affects physiological and biochemical properties such as enzyme activity, chlorophyll fluorescence parameters, and photosynthesis speed [10–12]. Salt stress severely impacts rice growth and yield worldwide [13]. Specifically, it causes physiological and biochemical damage, ion toxicity, disruption of normal metabolism, and inhibition of growth, ultimately affecting overall yield [14–16]. To enhance rice tolerance to salt stress, exogenous regulatory substances can be applied in appropriate amounts, helping to alleviate salt stress injury and improve tolerance [17,18]. Phytohormones, which serve as exogenous regulatory substances, are small-molecule chemical compounds vital for the development and growth of crops [19]. Widely used phytohormones are essential for adjusting crop-environment interactions [20], coordinating salt stress responses, and improving plant growth [21,22].

Phytohormones are essential for rice growth by controlling the plant's reaction to salt stress. The typical mechanisms of plant hormones alleviating rice salt stress are illustrated in Fig. 1. As shown in Fig. 1, phytohormones adapt rice to salt-stress environments by regulating physiological and biochemical processes [23–25]. Also, phytohormones boost rice's ability to tolerate salt by influencing gene expression [21,26,27], the synthesis of proteins [28], and salt stress signaling pathways [25,29]. Therefore, a systematic summary of the functions of various phytohormones in rice salt stress tolerance is essential for understanding the underlying mechanisms and optimizing the use of phytohormones for sustainable rice production.

This review highlights and examines the crucial roles of various phytohormones, such as abscisic acid (ABA), auxin (IAA), cytokinins (CKs), jasmonates (JA), gibberellins (GAs), melatonin (MT), salicylic acid (SA), ethylene (ETHY), and brassinosteroids (BRs), in alleviating the negative impacts of salt stress on rice. We provide a comprehensive overview of the inter-regulatory relationships between these phytohormones and salt stress, aiming to offer valuable insights into the use of exogenous phytohormone regulators to improve salt tolerance of rice and to elucidate the core mechanisms.
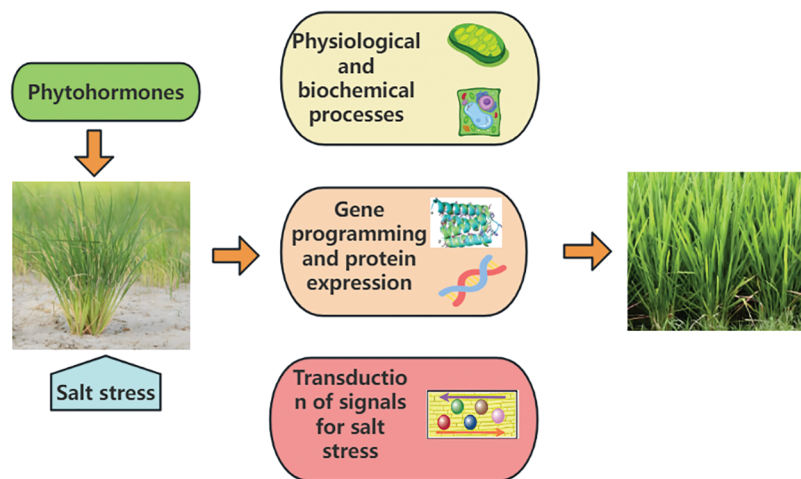

Figure 1: Illustration of typical mechanisms of phytohormones in alleviating salt stress in rice

2 Phytohormones and Salt Stresses

2.1 Abscisic Acid (ABA)

ABA is a phytohormone that plays a crucial role in helping plants adapt to environmental stresses like drought and salinity [30]. Numerous studies have shown that applying exogenous ABA enhances the salt tolerance of rice, including increasing the survival and growth of rice in saline conditions [31], enhancing rice's ability to withstand salinity, and boosting the yield of saline-alkali rice [32]. Some studies investigate the physiological mechanisms of how ABA alleviates salt stress in rice. For example, Gurmani et al. [33] showed that ABA promotes rice growth under salt stress by inhibiting the accumulation of sodium (Na^+) in rice shoots and reducing the sodium (Na^+)/potassium (K^+) ratio in rice genotypes. This may be because exogenous ABA improves the ion homeostasis of rice under salt stress by optimizing the ion transport-related signaling pathways [34]. Likewise, Chen et al. [35] demonstrated that applying ABA reduces the harmful impact of salt on rice by improving photosynthesis and modulating the antioxidant defense system, thereby enhancing ion balance and improving salt tolerance. Additionally, endogenous biosynthesis of ABA enhances the ability of rice seedlings to withstand salt stress by facilitating stomatal closure, ion exchange, and bettering water relations [36]. Furthermore, ABA-pretreated rice seedlings exhibited upregulation of 40 protein spots at the molecular level under salt stress conditions, which may be beneficial for enhancing salt tolerance. This may be because of the specific upregulation of many enzymes associated with energy metabolism, primary metabolism, and defense in rice seedlings pretreated with ABA. Moreover, ABA *de novo* biosynthesis enhances rice's resilience to salt stress by inducing strong *OsLea3* expression in rice roots [37].

Additionally, research has shown that the interactions between rice genes and ABA influence rice's response to salt stress. For example, the transcription factor OsNAC45 of NAC (NAM, ATAF1/2, CUC2) enhances rice salt tolerance by positively regulating the ABA signaling pathway [38]. Wang et al. [39] illustrated that miR528-AO, one of the target genes of miR528 in rice, can regulate the genetic expression associated with ABA metabolism and biosynthesis (including NCED2, NCED3, NCED5, ZEP, ABA8ox1, ABA8ox2, and ABA8ox3) under saline conditions. This regulation boosts ABA content, increases proline levels, accelerates reactive oxygen species (ROS) removal, and ultimately enhances rice's salt tolerance. Zhao et al. [40] demonstrated that OsCSLD4 is involved in rice's response to salt stress via the ABA-mediated osmotic regulation pathway. By overexpressing OsCSLD4, the expression of ABA synthesis genes in rice can be enhanced, ABA content can be increased, and rice's salt tolerance can be improved. Zhang et al. [41] indicated that OsIAA20, an Aux/IAA protein upregulated under abiotic stress conditions, is essential for rice's tolerance to salt stress by regulating an ABA-dependent mechanism. Furthermore, to explore the molecular pathways through which ABA enhances rice salt tolerance, Li et al. [42] and Yoshida et al. [43] demonstrated that ABA binding to PYR/PYL/RCAR receptors on the cell membrane inhibits protein phosphatase 2C (PP2C) activity. This inhibition activates SnRK2 kinase and it further phosphorylates the transcription factor ABF/AREB. The phosphorylated transcription factors enter the cell nucleus and initiate the expression of salt stress resistance genes, ultimately boosting rice salt tolerance. Table 1 summarizes the representative studies on ABA and related genes in alleviating salt stress in rice.

2.2 Auxins (IAA)

The plant hormone auxin, also known as indole-3-acetic acid (IAA), which influences essential aspects of plant cell division, elongation, and differentiation, is strongly correlated with the final shape and function of cells and tissues in plants [44]. In rice, IAA regulates and coordinates growth under stress conditions. IAA's response to salt stress mediates the regulatory network that links IAA signaling with salt stress [45]. IAA significantly contributes to lateral root development [46]. Meng et al. [47] indicated that IAA accumulation and dependent signaling can be influenced through biosynthesis and polar IAA transport,

thereby affecting lateral root formation in rice. IAA is crucial for the growth of rice when exposed to salt stress. On one side, reduced growth and development of rice under salt stress may result from the inhibition of IAA accumulation and response. For example, the reduction in IAA response due to salt stress is linked to inhibited root growth [48]. On the flip side, boosting the IAA content in the root system may enhance the root characteristics of rice under salt stress, thereby promoting growth [49]. The authors further demonstrated that elevated IAA content and a higher buffering capacity of IAA homeostatic processes may be critical for rice to tolerate salinity. Hence, the application of IAA may be a valid method to support the cultivation of rice under salt stress.

Many studies have been dedicated to revealing the intricate mechanisms through which IAA alleviates salt stress in rice. Applying IAA externally under salt stress conditions has been shown to enhance 1000-grain weight, grain filling rate, and yield by boosting the levels of starch, fructose, glucose, and sucrose in rice grains [50]. This may be attributed to the fact that exogenous IAA can mitigate the halophilic response of plant roots to salt [51]. Furthermore, IAA alleviates the harmful effects of salt stress on plants by boosting the antioxidant system and modulating the function of enzymatic antioxidants. Studies have shown that IAA can significantly increase the activity of α-tocopherol and the concentration of hydrogen peroxide (H_2O_2) in rice plants under salt stress [52]. This reason may lie in that IAA improves rice salt tolerance by optimizing antioxidant enzyme signaling pathways. In addition, some studies have shown that genes related to IAA production can be modulated to strengthen rice's ability to withstand salinity (Table 1). For instance, the overexpression of RCc3 increases the accumulation of IAA in roots by affecting local IAA biosynthesis and polar transport, thereby improving rice root structure, promoting plant growth, and enhancing tolerance to salt stress [53]. Chai et al. [54] showed that OsLAX and OsABCB auxin transporter genes are crucial in mediating crosstalk between salt stress and IAA signaling pathways, enabling rice to adapt to salt stress by regulating auxin distribution. Furthermore, some strains enhance the expression of the IAA efflux carrier gene OsPIN1 under salt stress, increasing the IAA concentration in rice and mitigating the negative impacts of salt stress, thus enhancing the growth characteristics of rice [55].

2.3 Cytokinins (CKs)

CKs are important hormones that primarily influence plant growth and development by controlling cellular division and morphogenesis [56,57]. CKs also affect plant defenses against abiotic stress like salt stress [58]. The relationship between plant resilience to salt stress and CKs has been investigated in various studies. CK biosynthesis and signaling mutants impact tolerance to salt stress, while salt stress affects the transcription of genes involved in CK signaling or homeostasis in rice [59]. Some research has shown that the upregulation of CKs can alleviate the harmful effects of salinity on rice. For instance, the application of exogenous CKs has been reported to enhance rice's salinity tolerance [50]. Joshi et al. [60] demonstrated that the inflorescence meristem-specific rice CKs oxidase OsCKX2 can regulate flower primordial activity under salt stress conditions by controlling CKs levels, thereby regulating rice grain yield. OsCKX2 knockout rice has higher relative water content and yield by accumulating CKs under salt stress.

However, it has also been shown that lowering CKs levels can favor salt tolerance in rice in some cases. For example, Li et al. [61] showed that the overexpression of AtUGT76C2, a CK glycosyltransferase, in rice reduces endogenous CK levels and promotes root growth, greatly enhancing rice adaptability to salt stress. Wang et al. [62] demonstrated that CKs-induced OsRR9 and OsRR10 genes function as negative regulators in response to salinity in rice. Additionally, the distribution of CKs is crucial in assessing the response of rice to stress. Yin et al. [63] emphasized that the overexpression of ARGONAUTE2 (AGO2) in rice increases CK content in roots and decreases it in shoots, enhancing salt tolerance. This occurs because AGO2 activates the expression of BG3, a potential CK transporter, altering CK distribution and ultimately regulating grain size

and salt tolerance in rice. Hence, optimizing the distribution of CKs is a proven technique to enhance both rice yield and salt resistance. Therefore, the role of CKs in salt tolerance in rice varies depending on the CKs species, as well as the related cells and tissue distribution.

2.4 Gibberellics (GAs)

GAs, a group of tetracyclic diterpene carboxylic acids, have a major impact on plant development, especially in seed dormancy and the processes of germination, leaf expansion, stem growth, and the formation of flowers and fruits [64]. Research has shown that GAs have a role in reducing salt stress in rice. The application of exogenous GA3 under salt stress conditions can elevate the germination rate, seed vigor, photosynthetic pigment, and protein content of rice, promote the growth of rice seedlings in salty environments, elevate rice yield, and strengthen salt tolerance [65,66].

Furthermore, a wealth of research has uncovered how GA3 helps rice cope with salt stress physiologically. For instance, exogenous GA3 application may counteract the detrimental effects of salt stress by affecting the lipid content and fatty acid unsaturation in rice chloroplast membranes during salt treatment [67], as well as by increasing the permeability of membranes and the nutrient content in rice leaves [65]. GA3 pretreatment helps improve ion balance, delay the loss of pigment accumulation, and enhance the antioxidant system of rice under salt stress, thereby improving the growth of rice seedlings under such conditions [68]. Salt stress reduces alpha-amylase activity by downregulating the expression of the alpha-amylase gene, inhibiting rice seed germination. The application of exogenous bioactive GA can enhance alpha-amylase activity to rescue rice seed germination under salt stress [69]. Moreover, Wen et al. [70] demonstrated that GA can mitigate the growth suppression of rice due to salt stress by regulating certain salt-regulating proteins. Furthermore, GA hormones can promote rice growth in conditions of salt stress by promoting cell multiplication and expansion [24], thereby alleviating the adverse consequences of salt stress on rice and improving its growth and development [71].

In addition, the synergistic effect of GA and certain genes can enhance salt stress resistance in rice (Table 1). For example, the positive effect of OsHAK9 on seed germination in saline conditions is partially based on elevated GA concentration. Disruption of OsHAK9 significantly reduces gibberellin 4 (GA4) levels, and exogenous GA3 partially rescues the oshak9a mutant's germination-deficient phenotype [72]. Furthermore, overexpressing OsGA2ox5, a gibberellin-metabolizing enzyme, boosts rice's salt tolerance by regulating GA biosynthesis and signaling [73].

2.5 Salicylic Acid (SA)

Phytohormone SA belongs to a class of phenolic compounds that function as endogenous growth regulators in plant seed germination, flowering, photosynthesis, the absorption and transport of ions, yield, and heat tolerance [74]. Additionally, SA is essential for plant defense mechanisms against both biotic and abiotic stresses, including salinity [75].

Under salt stress conditions, exogenous SA can promote the accumulation of nitrogen and dry matter in rice stems and sheaths in the short term and in the aboveground organs of rice in the long term [76]. Mostofa et al. [77] demonstrated that exogenous SA could alleviate oxidative damage in rice induced by salt stress by adjusting the antioxidant protection and glyoxalase functions. Furthermore, exogenous SA can increase the growth, germination rate, yield, and nutritional value of rice under saline conditions by inhibiting the accumulation of Na^+ and Cl^- ions and the increase in the activity of some enzymes (e.g., Superoxide Dismutase (SOD), Catalase (CAD) and Peroxidase (POD)) induced by salt stress [78]. Two later studies yielded similar results. Sheteiwy et al. [79] confirmed that SA attenuates the ionic imbalance caused by salt stress by reducing the accumulation of Na^+ and boosting the content of K^+ and Ca^+ in rice cells, promoting the germination of rice seeds, seedling growth, and nutrient absorption in plants, and enhances photosynthetic pigments, photosynthetic gas exchange, and chlorophyll fluorescence. Liu et al. [80] also

concluded that SA alleviates ion toxicity by reducing Na^+ content, thereby promoting the maintenance of reactive oxygen species and hormone homeostasis, facilitating starch hydrolysis, generating sufficient energy for seed germination, and ultimately improving the germination of rice seeds under saline conditions. From these studies, it can be inferred that SA may regulate ion homeostasis in rice under salt stress by optimizing ion transport signaling pathways, thereby enhancing rice salt tolerance.

Additionally, SA also induces the expression of several genes (Table 1), such as CAT, SOD, Autophagy Related Genes (ATG), Glutathione Peroxidase (GPX), Mitogen-Activated Protein Kinase 1 (MAPK1), transcription factor WRKY53 and Bax Inhibiotr-1 (BI-1), in rice seedlings. The SA pathway is essential for controlling autophagy and programmed cell death mechanisms, which are essential for salt tolerance in rice [81]. Studies suggest that SA can improve Rice's resilience to salt stress by upregulating the SA biosynthetic pathway gene (such as OsPAL, OsICS, and OsCM) expression levels under saline conditions [78].

2.6 Brassinosteroids (BRs)

BRs, isoprenoid-derived molecules that serve as unique polyhydroxy steroid hormones in plants, play a vital role in controlling plant metabolism, growth, and size. They are capable of sending endogenous signals that instruct plant growth and expansion [82]. BRs have proven effective in enhancing crop yields in saline environments [83]. The activated BR signaling pathway can reduce the negative impacts of salt stress on rice, and exogenous BRs have been shown to alleviate the inhibitory impact of salt stress on rice seedling development and the germination of seeds [84]. Anuradha et al. [85] showed that applying exogenous BRs can alleviate the harmful effects of salt stress on the germination of rice seeds, root elongation, and other growth processes by restoring pigment content and increasing nitrate reductase function.

Foliar spraying of rice seedlings with 24-epibrassinolide (EBL) can reduce oxidative stress by decreasing protein oxidation and lipid peroxidation and maintaining chlorophyll concentration, thereby restoring the development of rice seedlings under saline conditions [86]. Additionally, 28-homobrassinolide (HBL) and EBL can enhance rice's ability to withstand salt stress by enhancing growth parameters, protein and proline content, increasing the activity of various antioxidant enzymes, and decreasing malondialdehyde (MDA) content [87,88]. Similar studies have shown that EBL can significantly boost seed germination, and improve seedling morphological traits, and rice yield in conditions of salt stress by increasing rice antioxidant enzymes and K^+ maintenance in leaves and decreasing Na^+ content in rice roots and MAD content [89]. Therefore, BRs may enhance rice salt tolerance by impacting antioxidant enzyme signaling pathways and ion transport-related signaling pathways. Moreover, Sharma et al. [88] found that EBL can alleviate salt stress in rice by up-regulating BR (OsBRI1) genes. Similarly, Li et al. [90] demonstrated that BR enhances rice salt tolerance by inducing the dephosphorylation of the core transcription factor OsBZR1 under salt stress (Table 1).

2.7 Jasmonates (JA)

JAs, derivatives of fatty acids, are endogenous signaling molecules involved in various plant developmental processes. These include jasmonic acid (JA), methyl jasmonate (MeJA), jasmonic acid isoleucine conjugates (JA-Ile), and other key compounds [91]. Exogenous JA application [92] and the control of JA metabolism [93] have been shown to enhance rice tolerance under saline conditions. Exogenous JA effectively restored rice photosynthetic rate, seedling growth, leaf water potential, and dry matter in conditions of salt stress [92]. Foliar application of methyl jasmonate (MeJA) significantly improved leaf fluorescence, leaf gas exchange traits, and plant agronomic parameters in rice under salt stress [94]. MeJA can mitigate the negative effects of salt stress on rice by increasing plant growth, chlorophyll, and K^+ content [95].

Furthermore, exogenous JA application may affect rice salt stress by altering other endogenous hormones (e.g., ABA and GAs) in rice plants. For example, JA can increase the ABA concentration in

rice under salt stress and counteract the decrease in gibberellins caused by salt stress, thus enabling better adaptation to salt-stressed environments [96]. In addition, the interaction of rice genes with JA affects the response of rice to salt stress (Table 1). Ye et al. [97] showed that the overexpression of the JIOsPR10 gene, induced by JA, enhances rice's ability to withstand salt stress. Wu et al. [98] demonstrated that forms a transcriptional regulatory complex with OsNINJA and OsbHLH to control the expression of JA-responsive genes associated with salt tolerance in rice under saline conditions, thereby modulating the tolerance of rice to salt stress. Moreover, JA acts as a signaling molecule for inducing the rice PR10 gene. RSOsPR10, a novel PR10 protein, is induced by salt stress in rice roots through the activation of the JA signaling pathway, thereby enhancing rice's defense against saline conditions [99].

However, excessive activation of JA signaling can also have adverse effects. Some studies have shown that inhibiting JA signaling is important for enhancing salt tolerance in rice [100]. For instance, OsJAZ8 and its dominant-negative variant OsJAZ8ΔC, when overexpressed in the specific rice tissues, enhance salt tolerance in rice by suppressing JA signaling and other JA-dependent downstream genes under salt stress [101]. RICE SALT SENSITIVE3 (RSS3), a nuclear-localized protein that interacts with the transcription factors OsbHLH089 and OsbHLH094 to form a ternary complex that controls the salt-mediated elongation of rice root cells and promotes cell elongation by inhibiting the root JA response, thereby ensuring the development of rice roots when exposed to salt stress [102,103]. The conflicting results in the literature may be due to differences in the temporal and intensity patterns of JA accumulation and signaling, leading to varied responses to salt stress. Effective fine-tuning of JA signaling determines whether cells will adapt or undergo programmed cell death [104].

2.8 Ethylene (ETHY)

ETHY, a gaseous hormone with a simple C_2H_4 structure, regulates plant growth and development and plays a crucial role in various stress responses. The involvement of ETHY in plant responses to salt stress has been extensively studied. It has been reported that ETHY signaling regulates salinity responses by modulating ROS production and scavenging mechanisms [105]. Appropriate levels of ETHY can enhance plant salt tolerance by improving nutrient uptake, maintaining Na^+/K^+ homeostasis, regulating ROS, and increasing nitrate and sulfate assimilation under saline conditions [106].

ETHY plays a significant role in mitigating the inhibitory effects of salt stress on rice root growth. Research indicates that applying exogenous Ethrel (an ETHY-releasing agent) can significantly promote the growth of rice seedling root systems under salt stress. The improvement in these growth parameters helps rice better absorb water and nutrients in conditions of salt stress, thereby maintaining normal growth and development. ETHY also mitigates the adverse effects of salt stress by influencing the physiological characteristics of rice. Under salt stress, ETHY increases the activities of antioxidant enzymes in the rice root system, enhances the content of osmotic regulators, and decreases the content of MDA [107]. The improvement in these physiological properties helps rice mitigate oxidative damage and osmotic stress induced by salt stress, thus maintaining the integrity and stability of cell membranes.

In addition, several studies have demonstrated that increasing ETHY levels in rice can enhance its salt tolerance (Table 1). For example, the overexpression of OsARD1 increases the rate of endogenous ETHY release in rice, reducing its sensitivity to salinity [108]. Similarly, *Glutamicibacter* sp., a novel halotolerant plant growth-promoting rhizosphere bacterial strain, improves rice's resistance to salt stress by regulating ETHY production and reactive oxygen species accumulation, preserving ion homeostasis, enhancing photosynthetic capacity, and upregulating salt stress-responsive genes [109]. Moreover, rice SALT TOLERANCE1 (SIT1), a lectin receptor-like kinase, maintains the homeostasis of ETHY by enhancing MAPK3/6 protein kinase activity, thereby improving salt tolerance in rice [110].

However, some studies have shown that reducing ETHY levels can enhance salt tolerance in rice [111]. For example, 1-aminocyclopropane-1-carboxylate deaminase (ACCD)-producing *Streptomyces* sp. GMKU 336 reduces ETHY through the action of ACCD while helping plants scavenge ROS and balance ion content and osmotic pressure, thereby increasing salinity tolerance in rice [112]. Similarly, Sarkar et al. [113] found that *Enterobacter* sp. strain P23, a potent salt-tolerant ACC deaminase-containing plant growth-promoting rhizosphere bacterium, effectively protected the growth of rice seedlings under salt stress by reducing stress ETHY and reactive oxygen species, and by enhancing seed germination rate and seed vigor index. The differences in the role of ETHY biosynthesis in rice response to salt may be because only a single gene in the ETHY biosynthesis pathway is usually evaluated rather than the entire genes, and the optimal ETHY level required for normal rice growth may also be different in different stages of rice [114]. The appropriate amount of ETHY and signal intensity in rice response to salt stress may vary at different growth stages. Therefore, precise regulation of ETHY production and signal transduction may be crucial for improving rice salt tolerance. Further studies on the role of ETHY in rice resistance to salt stress are needed to clarify the differences in ETHY synthesis in alleviating salt stress.

2.9 Melatonin (MT)

MT, a lipophilic and hydrophilic biological indoleamine, plays a multifunctional role in plants. It regulates seed germination, promotes root growth, delays leaf senescence, and aids in plant growth and development under salt stress [115,116]. Exogenous application of MT is an advantageous strategy to improve the salt tolerance of rice plants. MT can increase both the dry and fresh weight of rice under salt stress, significantly reduce the accumulation of reactive oxygen species, and enhance salt tolerance [117].

Recent studies have investigated the physiological mechanisms by which MT enhances salinity tolerance in rice. Under salt stress, MT increases the relative water content, sucrose, and starch content by boosting the net photosynthetic rate and enhancing light energy absorption and transmission [118]. The application of MT increases rice yield by promoting the growth of vigorous green leaves with photosynthetic properties, enhancing the photosynthetic capacity and physiological activity of functional leaves, and protecting leaf cell membranes by preventing reactive oxygen species bursts and enhancing antioxidant activity [119]. Furthermore, MT improves rice plant tolerance to salt stress by (i) Activating antioxidants, regulating phytohormones, and promoting seed germination [120]. (ii) Improving nutrient accumulation and transport and regulating the ionic balance of K^+/Na^+ and Ca^+/Na^+ [121]. (iii) Decreasing chlorophyll degradation, inhibiting senescence-related genes, counteracting the accumulation of intracellular H_2O_2, and delaying leaf senescence and cellular death [122]. (iiii) Improving seed germination quality and root vitality, enhancing CAT and SOD activities in roots and leaves, and reducing Na^+ and Cl^- contents in roots and leaves [123].

In addition, MT can enhance rice salt tolerance by influencing specific genes (Table 1). For example, MT can increase salt tolerance by regulating the expression of OsHAKs to maintain Na^+/K^+ balance [119]. It also regulates K^+ balance by up-regulating the potassium transporter gene OsHAK5 at the root tip, ensuring better potassium retention and thus improving salt tolerance [124]. Xie et al. [125] showed that MT notably increased the expression levels of a distinct group of transcription factor genes, including 11 AP2/EREBP, 14 HB, and 3 WRKY genes, in rice seedlings under salt stress, activated multiple antioxidant pathways, and improved the abundance of metabolites such as gallic acid, butyraldehyde, AFMK, and isoquercitrin, which resulted in the improvement of salt tolerance in rice. Furthermore, The Salt Overly Sensitive (SOS) signaling pathway plays a crucial role in maintaining cellular ion homeostasis during salt stress. Exogenous MT influences the SOS pathway by regulating the expression of SOS genes, thereby alleviating salt stress in rice [126].

Table 1: Representative studies of phytohormones and related genes on mitigating salt stress and their effects in rice

Plant hormone	Related genes or proteases	Response of rice	Reference
Abscisic acid	Oslea3, OsCSLD4, OsIAA20	Mediated stomatal closure, ion exchange, and improved water relations; inhibited Na^+ accumulation in rice shoots and reduced Na^+/K^+ ratio in rice genotypes; improved rice photosynthesis and modulated the antioxidant defense system.	[33,35–37,40,41]
Auxins	RCc3, OsLAXs, OsABCBs, OsPIN1	Improved rice root structure, promoted rice plant growth; improved rice yield, 1000-grain weight and grain filling rate by increasing starch, sucrose, glucose and fructose contents in rice grains; abolished the halophilic response of rice roots to salt; increased the activity of α-tocopherol and increase the concentration of H_2O_2.	[49,51–55]
Cytokinins	OsCKX2, AtUGT76C2, OsRR9, OsRR10, AGO2	Regulate rice flower activity, Promoted rice root growth, relative water content and yield.	[60–63]
Gibberellic acid	OsHAK9, OsGA2ox7, alpha-amylase gene	Increased the germination rate, vigor index, photosynthetic pigment, and protein content; increased the membrane permeability and nutrient level of rice leaves; improved ion homeostasis and delayed the loss of pigment accumulation, enhanced the antioxidant system of rice plants; promoted the growth of rice seedlings and increase the rice yield.	[65,67–69,72]
Salicylic acid	OsCM, OsICS, OsPAL, CAT, SOD, GPX, MAPK1, WRKY53, BI-1, ATG	Promoted the accumulation of dry matter and nitrogen in rice stems and in the aboveground organs of rice; modulated the antioxidant defense and glyoxalase systems; reduced the accumulation of Na^+ and Cl^- ions and the activities of SOD, CAD, and POD; promoted rice seed germination, seedling growth, and plant nutrient uptake, and enhanced photosynthetic pigments, photosynthetic gas exchange, chlorophyll fluorescence, and yield.	[76–81]

(Continued)

Table 1 (continued)

Plant hormone	Related genes or proteases	Response of rice	Reference
Brassinosteroids	OsBRI1 OsBZR1	Restored pigment levels and increased nitrate reductase activity; reduced oxidative stress by reducing lipid peroxidation and protein oxidation and maintained chlorophyll concentration; enhanced rice antioxidant enzymes and K^+ maintenance in leaves; enhanced protein and proline content; decreased Na^+ content in rice roots and MAD content in rice seedlings; increased the germination rate, seedling morphological traits, root elongation, and rice yield.	[84–90]
Jasmonates	JIOsPR10, OsJAZ9, OsJAZ8, RSS3	Restored rice seedling growth, leaf water potential, and dry matter; improved leaf fluorescence, leaf gas exchange traits, and plant agronomic parameters; increased rice plant growth, chlorophyll, and K^+ content.	[92,95,97–99,101–103]
Ethylene	OsARD1, SIT1, MAPK3/6, ACCD, ACC	Increased the activities of antioxidant enzymes in the rice root system, the content of osmotic regulators, and decreased the content of MDA; regulated reactive oxygen species accumulation, maintained ion homeostasis; enhanced photosynthetic capacity, seed germination rate, and seed vigor index.	[107–110,112,113]
Melatonin	OsHAKs, OsHAK5, AP2/EREBP, HB, WRKY	Enhanced the photosynthetic capacity and physiological activity of functional leaves, and protected leaf cell membranes; increased both the dry and fresh weight of rice, seed germination, the relative water content, sucrose, and starch content; improved nutrient accumulation and transport, and regulated the ionic balance of K^+/Na^+ and Ca^+/Na^+; Decreased chlorophyll degradation, reduced the accumulation of reactive oxygen species, counteracted the accumulation of intracellular H_2O_2, and delayed leaf senescence and cell death.	[117–122,124,125]

3 Plant Hormone Crosstalk Regulates Rice Tolerance to Salt Stress

The interplay and crosstalk between various plant hormones are important for rice's tolerance to salt stress. This crosstalk helps rice adapt to such stress by regulating its morphological traits and mediating changes in hormone levels within roots, stems, and leaves [127]. ABA-mediated IAA transport regulates the formation of rice lateral root primordia (LRP), facilitating rice adaptation to mild salt stress conditions [128]. The synergistic effects of ABA and ET can mediate rice adaptation to salt stress, this may be because ABA and ET interact to control different mechanisms of rice root growth [129]. However, ABA and JA have antagonistic effects on salt stress-induced transcripts in rice roots [130]. Moreover, the JA/ET signaling pathway in rice roots is involved in the induction of RSOsPR10 (a root-specific gene) under salt stress, promoting root growth and root mass, thereby improving salt tolerance, while exogenous SA has an antagonistic inhibitory effect on it [131]. However, Liu et al. [69] showed that exogenous SA can improve the germination of rice seeds under salt stress by positively regulating the homeostasis of GA and ABA in rice under salt stress. In addition, exogenous MT boosts salt tolerance in rice by activating the IAA/ABA/BR signaling pathways, as well as the AP2/EREBP–HB–WRKY transcriptional cascade [125]. IAA and CK synergistically enhance carbohydrate accumulation in rice grains under salt stress. Exogenous IAA application increases IAA levels in the grains, subsequently raising CK levels and stimulating cell division, elongation, and enlargement, ultimately boosting grain weight, fruit set, and rice yield [50]. Hence the crosstalk effects of plant hormones are important for understanding and regulating rice response mechanism to salt stress.

4 Conclusions

Soil salinization poses a significant threat to rice. This study reviewed the role of various phytohormones, including ABA, IAA, CKs, GAs, SA, BRs, JA, MT, and ETHY, in rice's response to salt stress, both directly and indirectly. In many cases, exogenous applications of these phytohormones mitigate the negative effects of salt on rice. From the perspective of agricultural practice strategies, the type and concentration of hormones associated with the rice's growth stage and specific needs should always be taken into account, and this is because different hormones have unique mechanisms and effects. The timing and method of hormone application greatly influence its effectiveness, so it is important to determine the optimal application schedule considering the rice growth cycle and weather conditions. Particular attention is that the overuse of plant hormones can negatively impact rice, so the application dosage should be strictly controlled. Many studies on the role of phytohormones in rice response to salt stress have emerged over the years, however, the precise mechanisms by which phytohormones mitigate salt stress in rice remain incompletely understood in the current literature. The pathways, signaling processes and interactions with other physiological processes have not been systematically understood yet. Additionally, research on phytohormones primarily relies on traditional biochemical techniques, which have limitations in revealing the specific mechanisms. Future progress in further understanding the complex role of phytohormones in mitigating salt stress will depend on how to overcome these limitations. Future research could focus on the following directions:

- Mitigation effects of different types of phytohormones on salt stress in rice can vary, and the same hormone may have different effects at different concentrations. Therefore, it is interesting to screen for the most suitable combination of hormone types and concentrations for specific types of plants.

- Various ecological factors, such as soil type, climatic conditions, and irrigation methods, influence the response of rice to salt stress and the effectiveness of phytohormones. Therefore, the effects of these ecological factors are interesting to be examined in the future.

- Exploring the combination of different types of phytohormones and their combined regulatory effects on rice growth will provide valuable guidance for enhancing rice's resilience to future stress conditions.

- Identifying novel plant hormones or signaling molecules is of importance for regulating rice salt tolerance. Developing hormone analogs based on the structure and function of known hormones, and enhancing their activity and specificity to rice salt tolerance are important for future search.

- Investigations of new technologies and methods are beneficial for advancing plant phytohormone research. It is interesting to explore how to use high-throughput sequencing and gene editing technologies to more efficiently pinpoint and isolate genes and transcription factors associated with salt tolerance. Moreover, integrating smart agricultural technology, precision irrigation, and nutrient management with plant hormone regulation to enhance resource utilization and rice productivity under salt stress is also a promising direction. For further explorations.

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