



MINI REVIEW ARTICLE 

Chemical interventions to alleviate salt stress in cotton plants: A review

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Abstract

The alleviation of salt stress in cotton plants through the application of exogenous chemicals has emerged as a viable strategy to mitigate the adverse effects on various plant attributes, including growth, development, yield, and flowering. Plant hormones, known for their efficacy at low doses, have garnered significant attention in this context. Despite being inherently susceptible to salt stress, cotton plants experience severe impediments in water absorption from the soil, leading to delayed growth and development. Several phytohormones, including jasmonic acid, salicylic acid, and glycine betaine, have been extensively investigated in numerous studies for their potential to ameliorate salt stress in cotton plants. Promising results have been obtained with both foliar and seed treatments employing these substances. This foundational knowledge has paved the way for the development of alternative strategies to mitigate salt stress. However, the practical utilization of these chemicals is hindered by their elevated cost. Plant growth regulators, such as nitric oxide and melatonin, have also garnered interest for their ability to alleviate salt stress in cotton plants. Numerous studies have corroborated their effectiveness in this regard. This review comprehensively examines the aforementioned substances and extracts that have been investigated for their potential to mitigate the detrimental effects of salt stress on cotton plants.

Keywords

salt stress; cotton plant; plant hormones; foliar treatment; seed treatment.

Introduction

Salinity presents a growing global challenge, with its severity increasing annually (1). Regions particularly affected by salinity stress include coastal soils in southern Asia, the Pacific Ocean, and Australia. In India alone, approximately 6.73 million hectares of land have been impacted by salinity or sodicity (2). The issue of saline soil is also expanding within continental areas, exemplified by the rising salinity in areas near the Aral Sea in Uzbekistan over the past two decades (3). Consequently, it is imperative to conduct research on the impacts of various substances on cotton plants experiencing salt stress due to their economic importance. Cotton is regarded as a moderately salt-resistant crop, capable of thriving in soil with a salinity level of 7.7 dS m⁻¹. However, salinity exerts adverse effects on cotton growth, yield, and fiber quality. The detrimental effects of salt stress

are most pronounced during germination, emergence, seedling establishment, and later growth stages of cotton plants (4). Salt stress leads to delayed flowering, reduced fruiting duration, increased fruit drop, and decreased boll weight, all of which have cascading effects on seed yield (5).

balance, ion homeostasis, and the modulation of reactive oxygen species (ROS) levels (Fig. 1) (9).

In the following section, we elucidate the principal outcomes arising from the application of exogenous phytohormones, including jasmonic acid (JA), salicylic acid, glycine betaine, brassinolides, and various other botani-

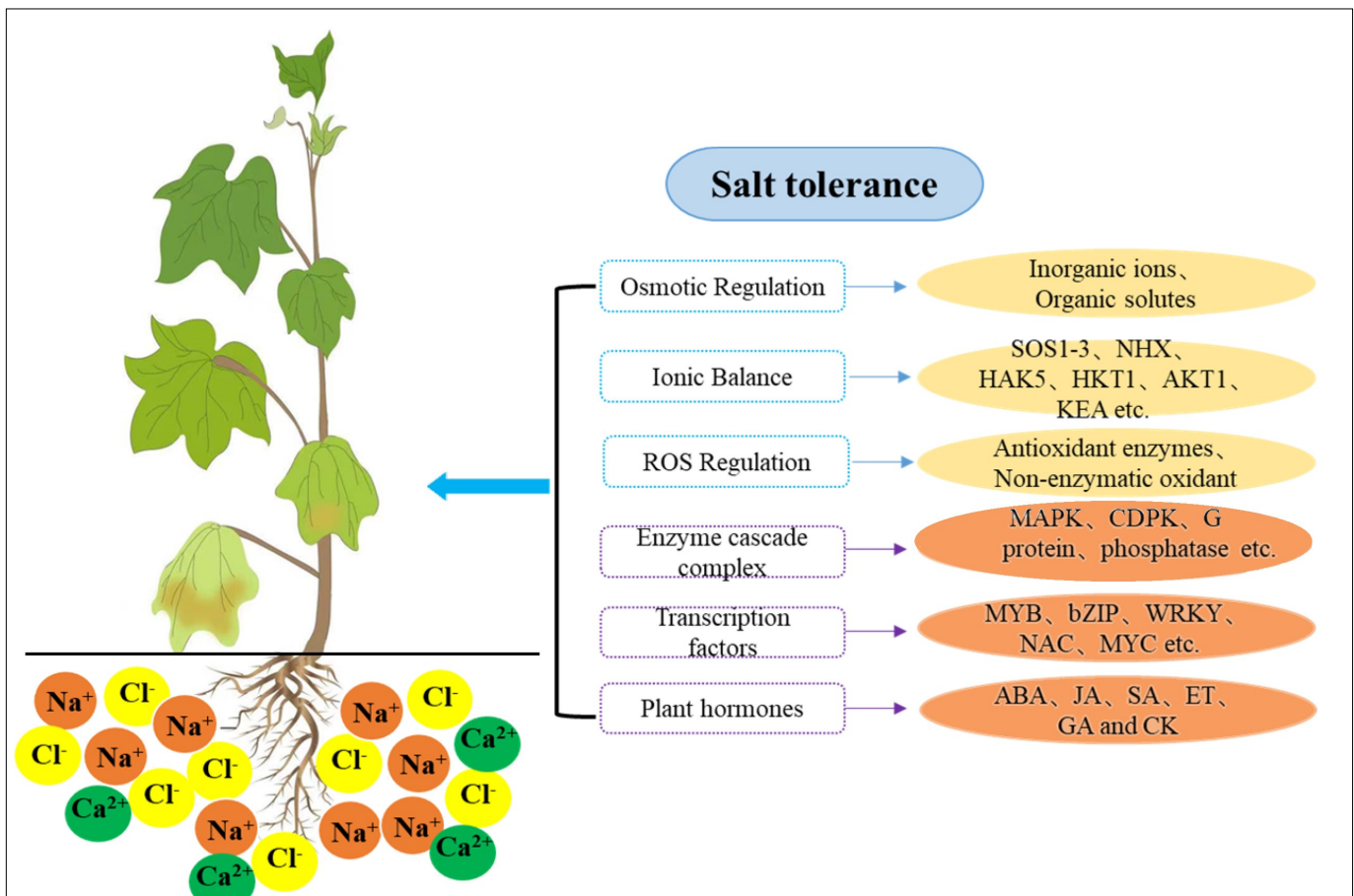


Fig. 1. The response of cotton plant to salt stress. A part of the figure was re-used from (9) with the permission of MDPI.

To mitigate these adverse effects, researchers have explored foliar and seed treatments in cotton plants. Foliar treatments aim to restore normal biological responses, while seed treatments are focused on enhancing germination and resilience against various abiotic stress factors. Plant hormones have gained attention due to their efficiency at low doses, and as such, they have been extensively investigated in the context of cotton plants. Notably, plant signaling molecules such as melatonin and nitric oxide have been subjects of review in another section of research.

Plant hormones

Exogenous plant hormones have been identified as key participants in the multifaceted mechanisms by which plants respond to salt stress (6). The application of exogenous plant hormones has emerged as an effective strategy to bolster the growth and development of cotton plants (7). The study of plant hormones has been extensively explored through genetic and molecular biology approaches, elucidating their profound impacts on various physiological aspects (8). In the context of combating salt stress, cotton plants deploy a repertoire of hormones, including jasmonic acid, salicylic acid, gibberellin, and cytokinin, in conjunction with enzymatic regulation of osmotic

cal compounds, to cotton plants or seedlings. The molecular structures of these plant-derived substances are depicted in Fig. 2.

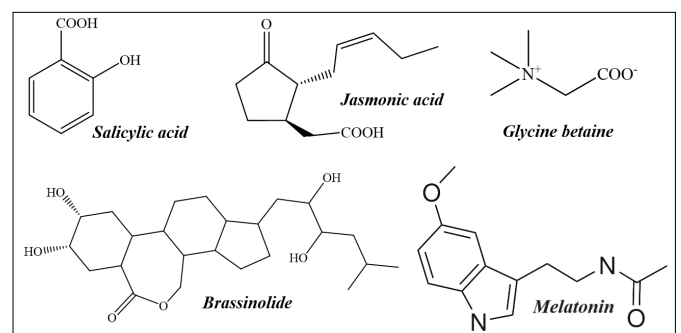


Fig. 2. The structure of plant substances the effects of which were studied on cotton plants tolerating salt stress.

Salicylic acid

Salicylic acid, a plant hormone, has attracted attention for potential exogenous application in enhancing plant responses to salt stress. Bile acid sodium symporter (BASS) genes, which encode sodium/solute symporters, play a crucial role in regulating plant salt tolerance. In response to salt stress, the expression of *GhBASS1* and *GhBASS3* genes was found to increase, positively contrib-

uting to salt tolerance in *Gossypium* species. When cotton seedlings were treated with specific concentrations of salicylic acid (2 mM), abscisic acid (1 mM), and gibberellic acid (0.5 mM) via foliar application, there was a significant up-regulation in the gene expression levels of *GhBASS1* and *GhBASS3*, either individually or together (10). Exogenous salicylic acid has been shown to optimize various physiological processes crucial for plant growth and develop-

Jasmonic acid

Jasmonic acid and jasmonates are considered to be a class of chemical compounds that potentially play a role in mitigating salt-induced stress in plants (14). It is hypothesized that jasmonic acid may contribute to enhancing salt stress tolerance in plants by modulating signaling pathways that lead to jasmonate-associated responses (Fig. 3).

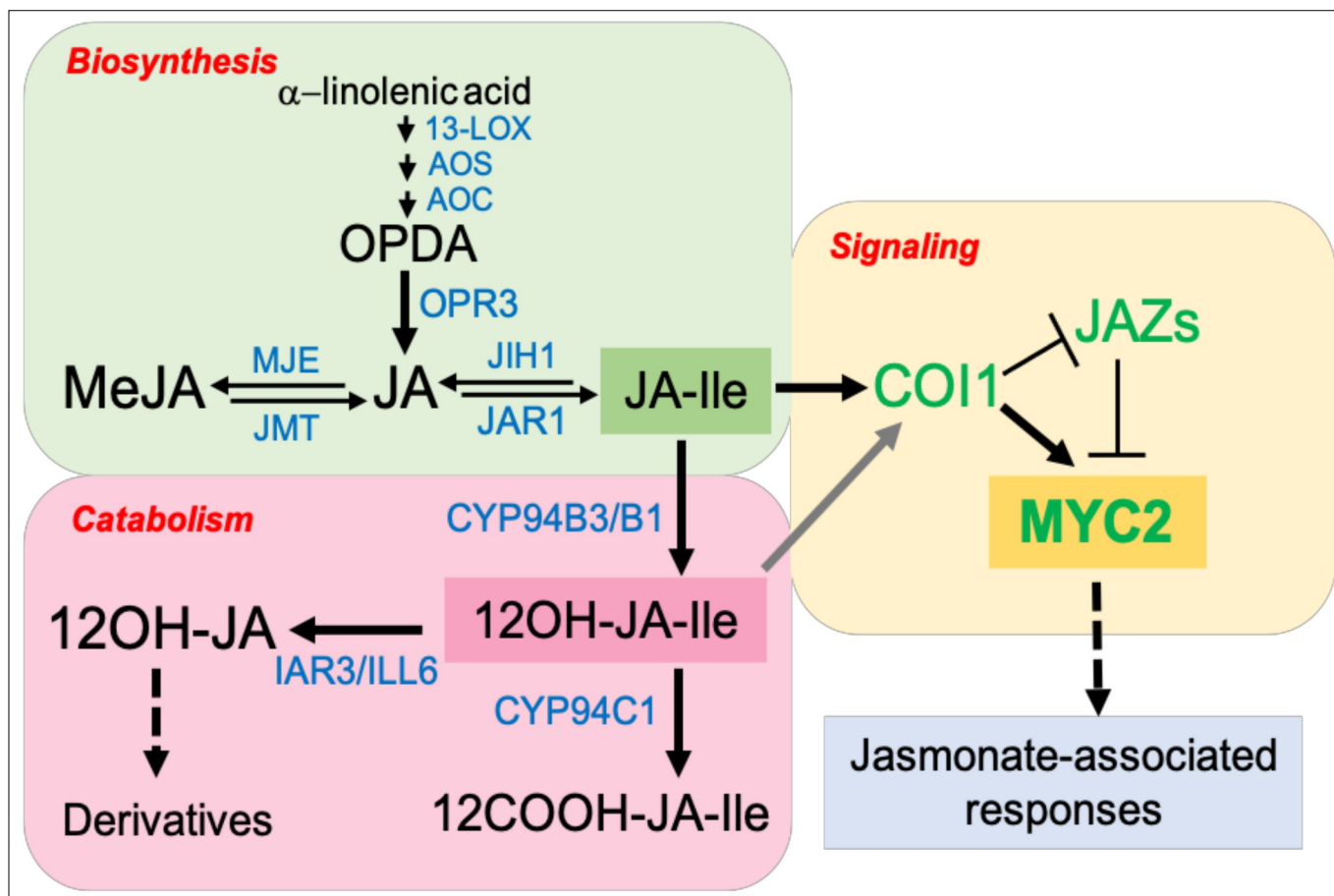


Figure 3. Overview of jasmonic acid biosynthesis and its signaling involved in plant salt tolerance responses. The Figure was re-used from (14) with the permission of MDPI.

ment. It enhances photosynthesis and the production of antioxidative compounds under salt stress by increasing the enzymatic activity of peroxidase, catalase, and superoxide dismutase (11). Furthermore, treating cotton seedlings exposed to 150 mM NaCl with 1 mM exogenous salicylic acid or 5 mM glycine betaine resulted in improved biomass accumulation. Notably, the nitrogen content in the dry biomass of both roots and shoots reached its highest level after treatment with 1 mM salicylic acid. Importantly, a negative correlation was observed between salicylic acid and sodium content; treatments with 1.5 and 2 mM salicylic acid resulted in lower sodium accumulation in plant biomass (12). Similarly, foliar application of salicylic acid promoted cotton plant growth. Treating plants with 1 mM foliar salicylic acid enhanced chlorophyll content and facilitated efficient gas exchange in cotton seedlings exposed to 150 mM NaCl-induced stress. There was a positive correlation between the net photosynthetic rate and chlorophyll b content following the application of salicylic acid (13).

Jasmonic acid treatment has been established as an effective approach for enhancing the growth and development of both water stress-tolerant and sensitive cotton cultivars. When combined with kaolin, JA treatment has demonstrated a heightened capacity to improve transpiration rates in cotton plants (15). Furthermore, JA treatment of cotton plant leaves has been observed to upregulate the expression of key genes associated with JA biosynthesis, specifically *GhOPR11*, *GhAOS6*, and *GhLOX3*. Consequently, this upregulation results in an increased abundance of the JA-isoleucine conjugate in the leaves. Additionally, JA treatment has been found to augment the hydraulic conductance of roots in well-hydrated conditions (16). These findings underscore the effectiveness of foliar JA treatment in mitigating abiotic stresses in plants, though it is worth noting that this efficacy has been demonstrated in plant leaves and not in seeds (14), (17).

Glycine betaine

Exogenous application of glycine betaine has emerged as a viable strategy for alleviating the adverse effects of salt

stress on cotton plants. Specifically, the application of a 5 mM dose of glycine betaine has been shown to enhance transpiration and photosynthetic rates, along with increasing intracellular CO₂ levels. Additionally, a positive correlation has been established between gas exchange parameters and stomatal characteristics, including stomatal density and length. Consequently, foliar application of glycine betaine is recommended as a promising approach to bolster stomatal function and promote plant growth under salt stress conditions (18). In a separate study, the foliar application of glycine betaine (5 mM) in combination with salicylic acid (1 mM) has demonstrated notable benefits in cotton seedlings subjected to salt stress. This treatment regimen resulted in an augmentation of chlorophyll content and the activation of antioxidative enzymes. Furthermore, a positive correlation has been observed between the net photosynthetic rate and the levels of chlorophyll a and b in treated samples growing under salt stress conditions. The concentrations of these chemical treatments have been determined to be optimal for mitigating the impact of NaCl-induced salt stress on cotton seedlings (13). Moreover, researchers have reported a reversal in the trends of ion uptake in cotton plants treated with exogenous glycine betaine and salicylic acid. Specifically, this treatment led to a decrease in Na⁺ level while increasing the uptake of K⁺, Ca²⁺, and Mg²⁺. This ion uptake modulation contributed to enhanced biomass accumulation (12).

Brassinosteroids

Brassinolides, a class of steroid-like phytohormones (Fig. 2), exert significant regulatory functions in plant metabolic pathways when plants are exposed to abiotic stresses, such as salt and drought stress (19). Their involvement in promoting fiber elongation in cotton plants has been well-established (20). In our extensive investigation into their role in enhancing salt tolerance in cotton plants, we found only one direct connection to the topic. Specifically, priming cotton seeds with 24-epibrassinolide, a type of brassinosteroid, has been reported as a viable approach to improve seed germination and promote growth when plants are subjected to salt and heat stress conditions. Furthermore, this treatment has been associated with the enhanced development of cotyledons and roots (21). However, it's noteworthy that combining brassinolides with other plant hormones such as abscisic acid, gibberellic acid, and auxin did not yield significant benefits under stress conditions.

Plant signaling molecules

Nitric oxide donors

Nitric oxide (NO) is a vital molecule with significant roles in numerous biochemical processes, particularly in mitigating the adverse effects of salt stress (22). Its involvement has been extensively investigated in various physiological functions, including nutrient uptake (23), photosynthesis (24), osmotic regulation (23, 25), redox processes, and more (26). In a study involving *Gossypium hirsutum* (cotton) leaves, foliar application of sodium nitroprusside (SNP), a nitric oxide donor, was found to delay leaf senes-

cence under salt stress conditions. The authors proposed that NO played a role in promoting cytokinin biosynthesis, which in turn affected leaf senescence. Three mechanisms were suggested to explain the delayed salt-induced leaf senescence in cotton following SNP application (24). Another study demonstrated that the treatment of cotton plants with 0.1 mM SNP and/or 0.1 mM salicylic acid led to enhanced rates of respiration, photosynthesis, and overall plant growth. Additionally, this treatment reduced the levels of hydrogen peroxide (H₂O₂) induced by salt stress from NaCl (27). NO generated from SNP was found to improve the efficiency of photosynthesis by enhancing water use efficiency and reducing the production of reactive oxygen species. A slow release of NO also supported the production of antioxidant enzymes such as catalase and superoxide dismutase, which played a crucial role in mitigating the toxic effects of NaCl (23). Furthermore, SNP treatment increased the content of potassium ions (K⁺) in cotton leaves exposed to salt stress, while sodium ion (Na⁺) levels decreased. This treatment led to a lower Na⁺/K⁺ ratio under NaCl stress conditions, directly contributing to osmotic balance by reducing sodium uptake (25).

Melatonin

Exogenous melatonin has been identified as a chemical compound that plays a significant role in enhancing salt stress tolerance in plants (28). In the context of cotton seedlings subjected to salt stress, the application of exogenous melatonin has been shown to mitigate the adverse effects by modulating the levels of reactive oxygen species (as depicted in Fig. 4). Specifically, this treatment resulted in reduced concentrations of malondialdehyde, hydrogen peroxide (H₂O₂), and superoxide anion (O²⁻), while concurrently increasing the activity of antioxidative enzymes and the levels of reducing agents, such as glutathione and ascorbic acid (29). Furthermore, the authors reported notable improvements in the biomass of cotton seedlings and the chlorophyll content following melatonin pretreatment. Exogenous melatonin was also observed to exert regulatory effects on the photosynthetic and fluorescence characteristics of cotton seedlings under conditions of salt stress (30). These observed effects were correlated with a reduction in the levels of chlorophyll degradation and mitigation of ion toxicity, as previously documented (28).

In a separate study, melatonin was found to mitigate the deleterious effects of salt-induced stress in cotton plants. This mitigation was achieved through alterations in the levels of H₂O₂, malondialdehyde (MDA), sodium (Na⁺), and chloride ions (Cl⁻). Furthermore, melatonin pretreatment resulted in an elevation of soluble sugars, proteins, and proline contents in response to salt stress. It was determined that a concentration of 20 μM of melatonin served as the most efficacious dose for enhancing salt stress tolerance and germination in cotton plants (31). The role of exogenously applied melatonin in modulating plant hormones and signaling molecules was linked to its ability to alleviate oxidative stress in cotton plants. Notably, melatonin was observed to regulate genes associated with redox processes, thereby contributing to the amelioration of salt-induced stress (32).

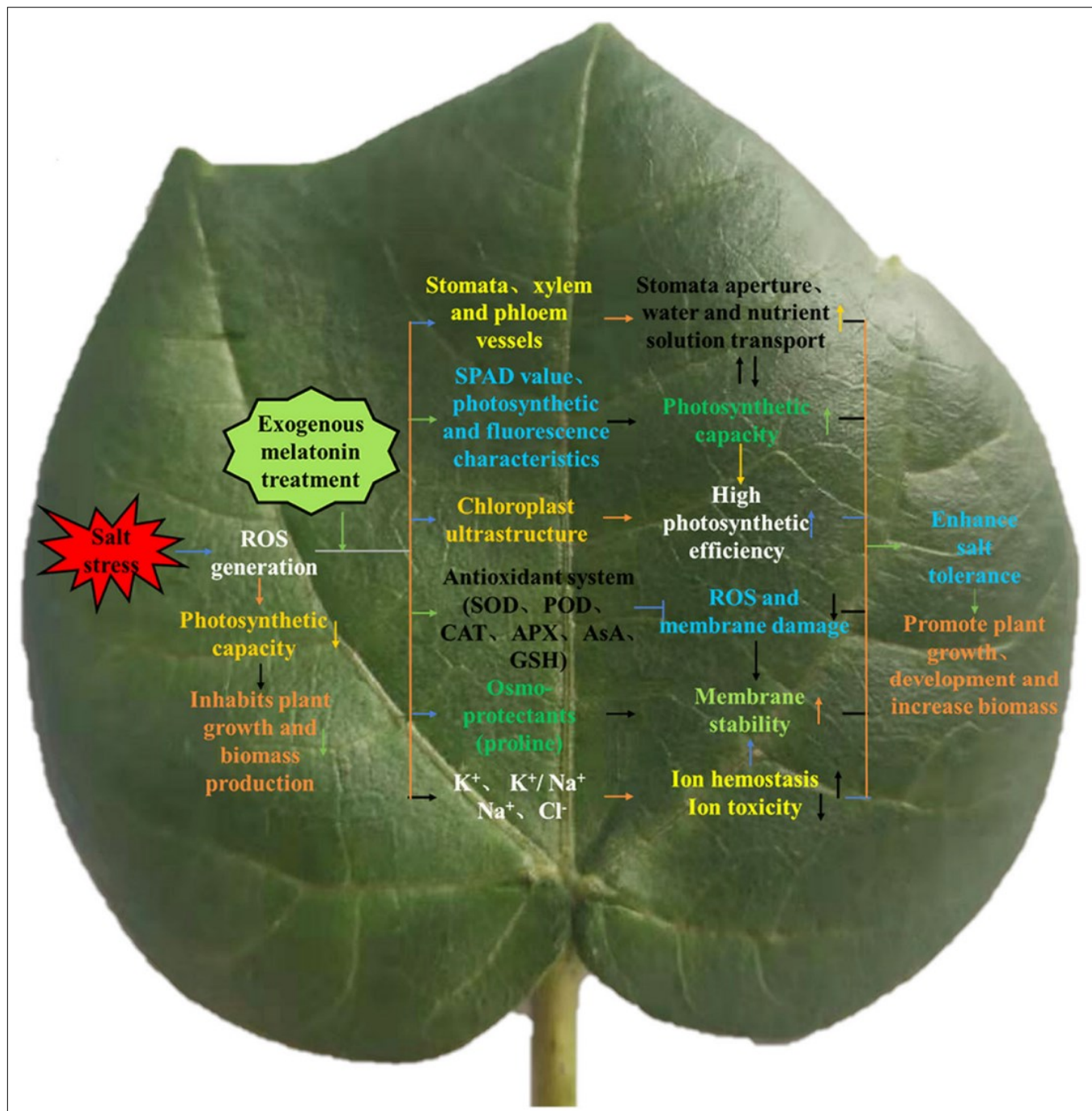


Fig. 4. Mechanism of action of melatonin that improves salt stress tolerance in cotton plant. The figure was re-used from (30) with the permission of Springer Nature.

Conclusion

Numerous plant compounds have been rigorously examined for their potential in mitigating salt-induced stress in cotton plants, with a primary focus on phytohormones such as salicylic acid, jasmonic acid, and glycine betaine. Additionally, significant attention has been directed towards signaling molecules, notably nitric oxide and melatonin, as potential strategies for ameliorating salt stress in cotton plants. Empirical investigations have substantiated the effectiveness of these chemicals, particularly when applied through foliar or seed treatments. Nevertheless, their practical application is hampered by their prohibitive cost. Nonetheless, the wealth of knowledge acquired through these studies has provided valuable insights into the mechanisms underlying salt

stress mitigation in cotton plants. Consequently, future research endeavors should be aimed at identifying economically viable alternatives that can be feasibly implemented in agricultural practices.

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Authors contributions

AA, MA – coordinated, drafted, and revised manuscript; MD, SE, AM, IB, NK – collected and analyzed literature, drafted manuscript; IM, ZB, IA – critically read and edited manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None.

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