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The Role of Nitric Oxide in Plants under Salt Stress: A Review

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Abstract

Salt stress poses a significant threat to agricultural productivity worldwide, necessitating a deeper understanding of plant responses to mitigate its detrimental effects. Nitric Oxide (NO) has emerged as a key signaling molecule involved in various aspects of plant growth, development, and stress responses, including salt stress. In this review, we provide an overview of the current knowledge regarding the role of NO in plants under salt stress conditions. We discuss the biosynthesis of Nitric oxide in plants, mechanisms by which NO mediates salt stress tolerance, including its involvement in ion homeostasis, osmotic adjustment, antioxidant defense, and gene expression regulation. Furthermore, we investigate the molecular mechanism that nitric oxide mediates under salt stress and the nitric oxide signalling under salt stress. We also discuss recent developments in our knowledge of the spatiotemporal dynamics of NO generation and activity under salt stress in several plant species and organs. Finally, we discuss the potential applications of NO-based strategies in improving salt stress resilience in crops and propose future research directions to unravel the intricacies of NO signaling in salt-stressed plants. This review aims to provide valuable insights into harnessing the regulatory functions of NO to enhance salt stress tolerance in crops, thereby contributing to sustainable agriculture practices.

Introduction

Various environmental stresses reduce the productivity of agriculture [1]. The global agricultural productivity is greatly affected by salt stress, which arises from various factors such as soil salinity, irrigation with saline water, and inadequate soil management. It disturbs the equilibrium of ions, triggers osmotic stress, and results in oxidative harm to plants, resulting in decreased growth, reduced crop yield, and compromised crop quality [2]. The disruption of ion homeostasis leads to an accumulation of sodium (Na^+) and chloride ions (Cl^-) in plant tissues. This accumulation hinders the uptake and transport of essential nutrients such as potassium (K^+), which in turn compromises important physiological processes like photosynthesis and protein synthesis. Osmotic stress diminishes the availability of water to plants, which in turn leads to water shortages and imbalances in osmotic conditions within cells. Plants respond to environmental changes by increasing the concentration of osmolytes such as proline and adjusting the opening and closing of stomata to ensure the maintenance of cell turgor pressure and the uptake of water [3]. Salt stress induces the production of ROS in plant cells, including superoxide radicals ($O_2^{\bullet-}$) and hydrogen peroxide (H_2O_2), which cause oxidative harm to cellular components like lipids and proteins, thereby worsening growth and productivity constraints [4]. The significant influence of salt stress on agricultural productivity leads to worldwide economic and food security consequences. Salt-affected soils hinder crop cultivation, resulting in lower yields, food scarcity, decreased

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farmer income, and dependence on imported food. To tackle the issue of salt stress, it is essential to adopt a comprehensive strategy that involves the development of crop varieties that can tolerate high salt levels, enhancing soil management techniques, and investigating alternative irrigation sources such as brackish water. Gaining knowledge about the mechanisms of salt stress and implementing strategies to reduce its impact can improve agricultural productivity, promoting global food security and sustainable agriculture [5].

NO acts as a crucial signaling molecule in plants, impacting growth, development, and responses to stress. NO is produced through both enzymatic (such as nitrate reduction by nitrate reductase) and non-enzymatic pathways [6]. It regulates 54 different biological processes, including as stress adaption, root formation, and seed germination. It interacts with a number of signaling molecules to control gene expression and protein function, including as reactive oxygen species and 31 phytohormones. The effects of NO are contingent upon its concentration, distribution, and cellular context, which can either promote growth or enhance stress defence mechanisms. Advancements in molecular genetics provide valuable understanding of the role of NO, offering potential advantages for enhancing crop productivity and promoting sustainable agriculture [7,8].

Given that 20% of cultivated land is impacted by salinity, it is crucial to comprehend the mechanisms for mitigating salt stress in order to maintain crop productivity and ensure food security [9].

NO as a signalling molecule: NO controls biological processes such as the balance of ions and the protection against oxidative damage [10]. Studying its role in salt stress provides important insights for enhancing plant salt tolerance.

Possible strategies involving Nitric Oxide (NO): Gaining insight into the role of NO in salt stress responses provides valuable knowledge for the advancement of innovative strategies such as the use of NO-releasing compounds or genetic manipulation to enhance salt tolerance in crops [11].

Interaction with other signalling molecules: Studying the interactions between NO and molecules such as phytohormones and reactive oxygen species reveals how NO can modulate plant salt stress responses [12].

Implications of sustainable agriculture: Comprehending the function of NO is essential in formulating sustainable methodologies that might mitigate the adverse effects of salinity on crop productivity, thus promoting environmental sustainability [13].

Mechanisms of NO-Mediated Salt Stress Tolerance

NO is essential for regulating ion homeostasis, especially during periods of salt stress. NO regulates ion transporters and channels as a means of modulating ion homeostasis. When exposed to high levels of salt, NO can increase the effectiveness of ion transporters that regulate important ion concentrations, such as potassium (K^+), while suppressing the activity of transporters responsible for absorbing sodium (Na^+) and chloride (Cl^-) [14]. This regulation serves to inhibit the build-up of noxious ions in vulnerable tissues, thus mitigating harm caused by excessive salt. NO plays a role in osmotic adjustment mechanisms by controlling the build-up of osmolytes, such as proline, glycine betaine, and sugars, within plant cells. Osmolytes play a crucial role in preserving cellular osmotic equilibrium and providing stability to proteins and membranes during periods of salt-induced stress. In addition, NO affects stomatal behavior, thereby regulating water loss from plant tissues. NO aids in water conservation and cellular hydration by promoting the closure of stomata. This, in turn, contributes to osmotic adjustment and enhances stress tolerance [15].

Mechanisms of Antioxidant Defence Facilitated by nitric oxide: Plants undergo an elevation in the production of ROS when exposed to salt stress, resulting in oxidative harm to cellular constituents. NO functions as a powerful antioxidant by effectively eliminating ROS and diminishing oxidative stress. In addition, NO increases the effectiveness of antioxidant enzymes such as Superoxide Dismutase (SOD), Catalase (CAT), and peroxidases [16]. These enzymes help remove ROS and safeguard plant cells against oxidative harm. NO aids in reducing oxidative stress caused by salt and helps maintain cellular balance by regulating antioxidant defence mechanisms. NO acts as a signalling molecule to regulate gene expression in response to salt stress [17]. It controls the activity of stress-responsive genes that are responsible for regulating ion transport, producing osmolytes, and defending against oxidative damage. In addition, NO modulates the activity of transcription factors and protein kinases, which regulate the expression of genes related to stress. NO facilitates alterations in gene expression, enabling plants to adjust to salinity stress and improve their resilience to unfavourable environmental conditions [18].

Biosynthesis of Nitric Oxide (NO) under salinity stress

The Nitric oxide (NO) is produced primarily through oxidative and reductive pathways in plants. L-arginine, oxygen, and NADPH are transformed into NO and citrulline via the action of NO Synthase (NOS) in the oxidative route; however, it is still unclear whether NOS exists in plants or what it looks like. At first, it was believed that Arabidopsis NO-Associated 1 (AtNOA1) exhibited NOS activity; however, later investigations revealed that this was not the case, leaving the identity of NOS in plants unclear [19]. In reductive pathways, nitrite is the main substrate that is reduced to NO, and enzymes like Nitrate Reductase (NR) and plasma membrane-bound Nitrite-NO Reductase (Ni-NOR) are essential for this pathway [20].The inner membrane of the mitochondria can potentially take part in the reduction pathways of NO production (Figure 1).

Nitrate reductase catalysed production of NO

Multiple investigations have validated the function of cytoplasmic Nitrogen Reductase (NR) in the synthesis of NO in plants under diverse biotic and abiotic conditions, as well as during physiological activities. The primary role of NR, which is found in the cytosol, is to transfer two electrons from NAD (P) H to nitrate, which is then reduced to nitrite (+3). On the other hand, in aerobic Nitrate Reductase uses nitrite as a source [21].

NO synthesis from L-arginine

Nitric oxide synthase, or NOS, is necessary for the production of NO in animals. In mammals, three distinct isoforms of NOS have been found. L-arginine's five electron oxidation to L-citrulline and NO is catalysed by them and is dependent on NADPH. The most contentious mechanism in plants is the arginine-dependent one, which involves the NOS enzyme. After years of research, there is still no concrete molecular proof that NOS is present in plants, but there is some indirect evidence of NOS-like activity that is susceptible to NOS inhibitors in animals [22].

Role of polyamines and hydroxyl amines in NO production

The function of polyamines in NO production has been well documented. In 2006, the first proof that polyamines contribute to the generation of NO was presented. It was discovered that exogenous Spermine (Spm) and Spermidine (Spd) induced rapid NO production in Arabidopsis [23].

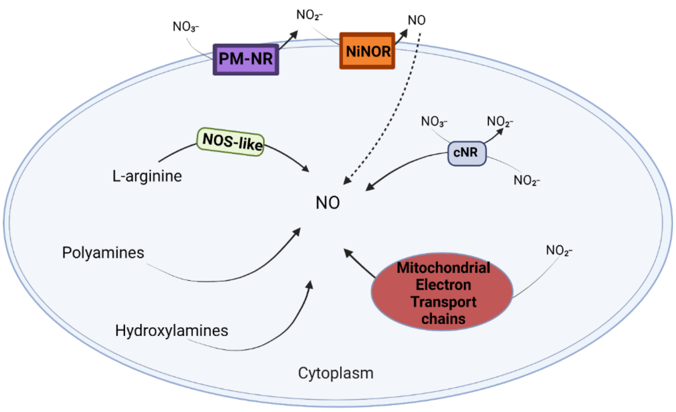

Figure 1: Various pathways involved in NO biosynthesis in plants.

Action of NO in plants under salt stress

The range of NO activity is extremely wide. It is engaged in numerous physiological and biochemical processes that occur in plants during their growth and development, serving as a signaling molecule in the process. NO plays role in stomatal movement, flowering period, seed germination, and flower development. It functions as a gaseous molecule in plant defence systems against biotic and abiotic stressors, including pathogen infections, dehydration, salt stress, high temperatures, UV radiation, hypoxia, wounds, and UV radiation [24].

NO participation in the reactions of plants to salt stress

NO reduces the harm induced by exposure to salt through a number of methods, which are outlined below and shown in Figure 2.

Maintaining Ion hemostasis: Elevated salt stress in plants can cause an excess of sodium ions (Na^+) to accumulate and deplete the potassium ion (K^+) pool, disrupting intracellular ion homeostasis and resulting in ion toxicity. Maintaining an optimal Na^+/K^+ ratio is crucial to prevent ion toxicity as well as intracellular osmotic pressure, membrane potential, and cytosolic enzyme activity. NO is essential for maintaining plant ion homeostasis in salinized conditions. Through controlling ion channel function, it aids in the excretion of Na^+ from plants or its sequestration into vacuoles. Certain halophytes exhibit how NO stimulates the growth of salt glands that release Na^+ from the cell [12]. In order to maintain the K^+/Na^+ balance, wheat, rice, and show increased endogenous NO levels and selective K^+ and Na^+ transport [25]. Under salt stress, NO increases the activity of vacuolar H^+-ATPase and H^+-PPase, which supply the energy for Na^+/H^+ exchange in seedlings of maize and wheat leaves [26].

Inducing seed germination: Due of its ability to prevent seed germination, salt seriously reduces agricultural productivity. The application of SNP under salty conditions has been demonstrated in multiple instances to boost the % germination of a variety of plant species, including wheat, rice, and *Eucalyptus urophylla*. According to a different study, NO mostly increased beta-amylase activity, It stopped wheat seeds exposed to salt stress from declining in germination index, germination percentage, vigor index, and imbibition rate. Rice seed germination is reduced by salt when low NO concentrations are present, and the opposite is true when high NO concentrations are present [27-29].

Absorption of nutrients: Plant's ability to absorb nutrients is impacted by salt, but their ability to absorb beneficial nutrients is enhanced when exogenous NO is applied. It is found that NO increased the Nitrogen (N) content in rice leaves and reduced the salt stress effect on the biomass accumulation and plant height. In order to mediate NH_4^+ transport, NO also controls the expression of NH_4^+ transporters, which may represent N absorption and its subsequent utilisation [30].

Efficiency of photosynthetic reactions: By lowering stomatal conductance, photosynthetic rate, and chloroplast activity, salt stress has a substantial detrimental effect on photosynthesis. Many of these negative effects on photosynthetic machinery have been demonstrated to be inverted by NO [31].

Respiration rate: Plants have a distinct respiratory terminal oxidase known as Alternative Oxidase (AOX), which catalyses cyanide-resistant respiration and affects salt-stress responses. In order to mitigate the oxidative and photosynthetic damage brought on by salt exposure, Salt stress amplifies both the cyanide-resistant respiration rate and the expression of AOX genes, which NO enhances [32].

Maintain Osmotic Balance: Low water potential brought on by excess the concentration of salt in the environment causes osmotic stress in plants. Plants gather osmotic materials in the cytoplasm for osmoregulation, such as charged metabolites (proline and glycine betaine), polyols (like mannitol and sorbitol), simple sugars (sucrose and fructose), and complex sugars [33].

Reduction of Oxidative stress: When subjected to salt stress, Reactive Oxygen Species (ROS) such as superoxide, Hydrogen Peroxide (H_2O_2), hydroxyl radicals, and singlet oxygen quickly build up. ROS function as signalling molecules to trigger salt stress reactions when present in low quantities, but when present in excess, ROS can result in oxidative damage. Elevated levels of Reactive Oxygen Species (ROS) within cells have the potential to adversely affect multiple physiological functions, such as DNA damage, protein denaturation, lipid peroxidation, and aberrant carbohydrate build up. Such cellular damage may result in suppression of plant growth. As a result, plant cells have evolved highly developed enzymatic and non-enzymatic antioxidant defense mechanisms to scavenge abundant Reactive Oxygen Species (ROS) and maintain appropriate redox conditions within cells [34]. Non-enzymatic scavengers include GSH, alkaloids, proline, alpha-tocopherol, carotenoids, phenolics, flavonoids, and Ascorbic Acid (ASA). Some examples of enzymatic scavengers are peroxidase, Catalase (CAT), Guaiacol Peroxidase (GPX), GSH Reductase (GR), Ascorbate Peroxidase (APX), and Superoxide Dismutase (SOD) [35].

Programmed Cell Death (PCD): Old, damaged or undesired cells are eliminated by PCD in order to preserve cellular equilibrium. PCD develops in plants in response to both biotic and abiotic stressors as well as during growth [36]. It has been found that mustard plants treated with salt, and NO reduced PCD [37].

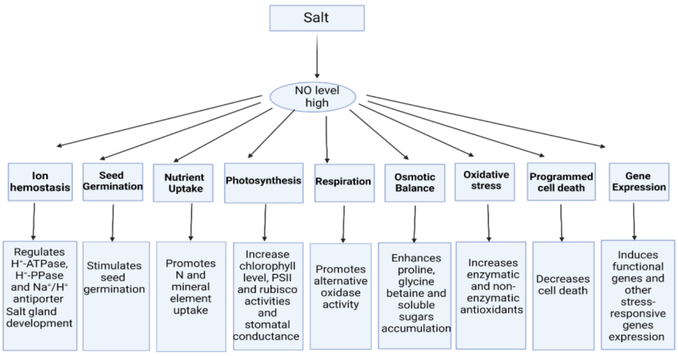

Figure 2: Different mechanisms used by NO to mediate salt tolerance.

NO Signalling in Salt Stress Conditions

For plants to grow and develop, a variety of tiny active chemicals are essential, including melatonin, Carbon Monoxide (CO), Polyamines (PAs) etc. These chemicals, along with NO, are crucial for integrating salt signaling because they control a number of different metabolic processes.

Additionally, evidence have shown that phytohormones and NO work together to affect salt tolerance through regulating a number of physiological and biochemical pathways, including photosynthesis, mineral nutrient balance, antioxidant metabolism, and osmolyte accumulation.

NO and Active Substances with Small Molecules

Polyamines: Plants contain large amounts of aliphatic polyatomic compounds, or PAs. Researches have indicated that plant's ability to withstand salt is enhanced when PAs and NO interact. It has been reported that under salt stress, NO increases the activity of PA biosynthesising enzymes, such as arginine decarboxylase and S-adenosylmethionine decarboxylase [38]. Also, NO controls the amount of free PA in cucumber seedlings, improving their resistance to salt [39].

Carbon Monoxide (CO): It was discovered recently that CO, through a NO-mediated signalling mechanism, improves wheat's ability to withstand salt. Utilizing an aqueous solution 50% CO-saturated was one way to increase salt tolerance. PM H^+-ATPase and antioxidant enzyme activity rose as a result. In CO-treated salt-stressed seedlings, endogenous NO quickly rose at the tips of their roots. cPTIO therapy, however, nearly totally prevented CO-induced NO generation. These findings imply that CO, via a NO-dependent mechanism, can mitigate damage caused by salt [40].

Melatonin: Melatonin is a tiny molecule that functions as an antioxidant and free radical scavenger in stressed environments. Numerous studies have demonstrated the strong relationship between melatonin and NO in plants' salt responses. It was observed that rapeseed growth inhibition caused by salt was alleviated by exogenous application of melatonin and SNP, which decreased Na^+ buildup. Melatonin, however, was unable to cure the Atnia1/2 and Atnoa1 mutant plants' sensitivity to salt [41].

Sulphur: Following nitrogen, phosphorus, and potassium, sulphur ranks as the fourth most essential nutrient required by plants. The combined protective effect of sulphur and NO on plants against severe salt-induced damage has been well explored. It has been shown that by regulating the H^+ pump and Na^+ transporter functions in leaves and roots, the administration of NO and S reduced the concentrations of Na+ and Cl^-. Furthermore, increasing the amount of NO and S in plants boosted the activity of the enzymes CAT, APX, and GR that scavenge ROS. Moreover, mustard leaves treated with NO and S expanded their stomata, improving photosynthetic capacity. These results suggest that NO and S cooperate to enable plants to withstand salinity [42].

Phytohormones and NO

Recent research on plant hormones and salt stress responses has shown a strong link between NO and signal transduction.

Auxin: Auxin, the first hormone discovered in plants, is essential to their growth, development, and responses to salt stress. According to one study, foliar application of the bioactive auxin indole-3-acetic acid (IAA) preserved membrane stability and increased chlorophyll content in salt-stressed maize plants [43].

Cytokinin: The way that plants react to salt stress is influenced by CK. For instance, by regulating the expression of the gene that removes Na^+ from the root xylem, Arabidopsis high-affinity K + transporter 1; 1, modulates the accumulation of Na^+ in the shoot. This regulation is reliant on transcription factors in the CK signalling pathway, including ARR1 and ARR12 [44].

Gibberellic acid: Gibberellic acid is a well-known phytohormone that promotes growth and development in plants and controls their reactions to stress. Through the destruction of DELLA transcriptional repressor proteins regulated by the proteasome, GA stimulates growth. Due to its hypersensitivity to salt, the *Arabidopsis della* double mutant suggested that GA had a deleterious effect on salt responses [45]. It was observed that shown that RGL3, a DELLA protein, and IAA17 were stabilised by salt-induced NO, which led to a decrease in the amount of bioactive GA4. Moreover, it was demonstrated that RGL3 and IAA17 interacted and stabilised one another, enhancing resistance to salt stress [46].

Salicylic acid: Widely distributed in higher plants, SA is a phenolic molecule that has a role in the regulation of plant physiology, systemic defences, and responses to abiotic and biotic stress. It was observed that SA enhanced the accumulation of glycine betaine to shield the mung bean photosynthetic system from salt stimulation [47]. When SA or NO was given to salt-stressed *V. angularis*, the accumulation of proline, glycine betaine, and sucrose avoided organelle destruction. Furthermore, the exogenous infusion of SA and NO decreased oxidative stress, improving the growth and photosynthetic efficiency of *V. angularis*. These findings demonstrate that the application of SA and NO promoted biomass accumulation and growth [48].

Jasmonic acid: Abiotic stress-related damage is largely prevented by JA, and NO has an impact on JA production and signalling pathways. Application of JA and NO, either alone or together, has been found to enhance osmolyte production, metabolite accumulation, and antioxidant metabolism. It has been observed that JA signaling deficiencies inhibited the NO-dependent activation of specific plant defensive responses to salt stress in Arabidopsis [49].

Abscisic acid: In response to a variety of adverse stressors, such as salt, ABA shields plants. Researchers discovered that ABA and NaCl could promote both. Exogenous SNP treatment is shown to greatly boost endogenous ABA synthesis in salt-stressed wheat seedlings. Other researchers discovered that

NO might function downstream of ABA. For example, tobacco plants' tolerance to salt and ABA levels were increased by NCED overexpression. Additionally, it promoted the transcript and activity levels of SOD, CAT, APX, and GR, as well as the generation of NO and hydrogen peroxide by NADPH oxidase and a NOS-like enzyme [50].

NO signalling - Molecular mechanism

One important signalling molecule that is essential for plant resilience to salt stress is NO. There are Cyclic Guanosine Monophosphate (cGMP)-dependent and -independent mechanisms that resemble the NO signalling pathway in mammals. Low NO concentrations trigger the cGMP-dependent pathway, which is catalysed by soluble guanylate cyclase and involves the transformation of GTP to cGMP. Studies on the cGMP-independent path have led to the identification of several S-nitrosylated proteins, including significant regulatory/signaling proteins that control plant development and stress responses [51] (Figure 3).

cGMP: It has been demonstrated that the NO-cGMP signaling pathway plays a significant role in the defense mechanisms activated by salt stress. The NO-cGMP cascade in root nodules of soybean was stimulated exogenously by the antioxidant caffeic acid, which led to the scavenging of ROS to reduce salinity-induced oxidative stress. This phenomenon suggested that NO-cGMP signalling is involved in plant responses to salinity.

Protein S nitrosylation: S-nitrosylation is a redox-based posttranslational modification of proteins that is the primary mechanism by which NO performs its physiological activity. A system that has been preserved throughout evolution, protein S-nitrosylation controls several facets of cellular signalling. When NO is combined with cysteine residues, S-Nitrosothiols are created. This process modifies the properties of the changed proteins, such as their stability, subcellular localization, enzymatic activity, and protein-protein interactions. It was found 49 proteins that were S-nitrosylated differently in citrus leaves treated with NaCl [52]. A recent study demonstrated that in saline conditions, the S-nitrosylation of Cys-374, a DELLA protein, in Arabidopsis RGA inhibited its degradation by the proteasome. It has been suggested that NO negatively modulates GA signalling via the S-nitrosylation of RGA to balance the growth and stress responses because the accumulation of RGA subsequently retards growth but increases salt tolerance [51].

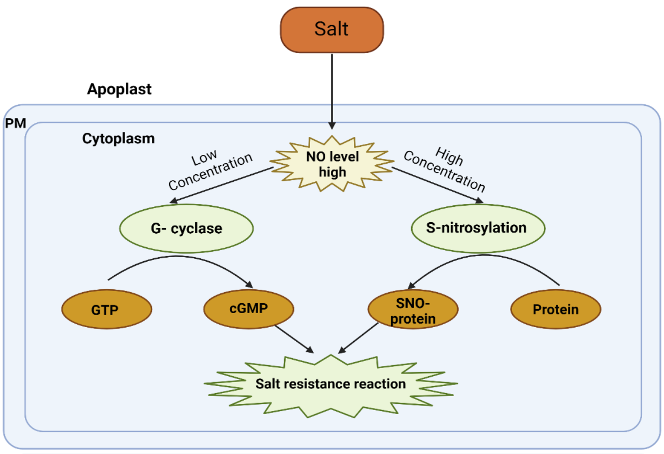

Figure 3: Different mechanisms used by NO to mediate salt tolerance.

Conclusion

NO is a widely distributed bioactive molecule that is crucial to a wide range of physiological functions in plants. NO functions in plant defense processes as a signaling molecule as well as in growth and development as a substance with hormonal properties. The production of cGMP, protein post translational modification are intracellular signaling responses to NO, linkage of NO, phytohormones and other signal transduction molecule during salt stress condition are investigated, but the exact biochemical and cell biological makeup of these reactions is frequently yet unclear. The chemistry, production, physiological functions, and signalling pathways of NO in plants are now being studied by a large number of researchers, further research are required to identify the direct target of nitric oxide.

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