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Interplay between nitric oxide and sulfur assimilation in salt tolerance in plants



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ARTICLE INFO

Article history:

Received 18 September 2015

Received in revised form

15 January 2016

Accepted 15 March 2016

Available online 1 April 2016

Keywords:

Abiotic stress

Antioxidant system

Glutathione

Plant hormones

Sulfur

Signaling

ABSTRACT

Nitric oxide (NO), a versatile molecule, plays multiple roles in plant growth and development and is a key signaling molecule in plant response to abiotic stress. Nutrient management strategy is critical for abiotic stress alleviation in plants. Sulfur (S) is important under stress conditions, as its assimilatory products neutralize the imbalances in cells created by excessive generation of reactive oxygen species (ROS). NO abates the harmful effects of ROS by enhancing antioxidant enzymes, stimulating S assimilation, and reacting with other target molecules, and regulates the expression of various stress-responsive genes under salt stress. This review focuses on the role of NO and S in responses of plants to salt stress, and describes the crosstalk between NO and S assimilation in salt tolerance. The regulation of NO and/or S assimilation using molecular biology tools may help crops to withstand salinity stress.

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Peer review under responsibility of Crop Science Society of China and Institute of Crop Science, CAAS.

<http://dx.doi.org/10.1016/j.cj.2016.01.009>

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1. Introduction

The exposure of plants to high salt concentration creates ionic toxicity due to the accumulation of Na^+ and Cl^- ions, which impair growth and development of plants. The accumulation of Na^+ ions in excess is largely responsible for the reductions in growth and yield under salinity. Salt stress disturbs the nutritional homeostasis of minerals [1], causes membrane damage, inhibits enzyme activity, and alters levels of growth regulators and metabolic activity [2,3]. Salt stress induces reactive oxygen species (ROS) production and causes damage to cellular components, membrane lipids, proteins, and nucleic acids [4]. To prevent the effect of excess ROS production, plants develop multiple detoxification mechanisms. The best-studied mechanism is the induction of antioxidant systems, but the mechanism of enhancement of sulfur (S)-assimilation that induces the production of S compounds via the increased activity of ascorbate–glutathione pathway (AsA–GSH) enzymes has recently been suggested as a response to salt tolerance [5–7].

S is the fourth major essential plant nutrient element after nitrogen (N), phosphorus (P), and potassium (K) [6]. S deficiency substantially limits crop productivity. S is an integral part of major metabolic compounds, such as amino acids, methionine and cysteine (Cys), GSH, Fe–S clusters, sulfolipids, glucosinolates, vitamins (biotin and thiamine), coenzyme A, and the thioredoxin system, which regulate physiological processes and raise salt tolerance [5,6]. A critical concentration of S regulates chlorophyll content, N content, activity of photosynthetic enzymes, protein synthesis, and the electron transport system [6], and appropriate availability of S determines photosynthetic function under optimal and stressful environments and potentially mitigates salt-induced oxidative stress [5,7–9]. Studies of Nazar et al. [7] and Fatma et al. [10] have shown that S supplementation improved the photosynthetic efficiency of plants under salt stress via increased GSH production and activity of enzymes of the AsA–GSH cycle. GSH is a major source of non-protein thiols and acts as an important non-enzymatic antioxidant. The antioxidant system participates in stress resistance and amino acid transport across membranes [11] along with fulfilling other roles associated with redox sensing and signaling and provides protection against salt stress.

Phytohormones are chemical messengers derived from plant biosynthetic pathways that act at the site of their synthesis or are transported to some other site in the plant to mediate growth and developmental responses under both optimal and stressful environments [12,13]. There are five groups of phytohormones: auxin, gibberellins, ethylene, cytokinin (CK), and abscisic acid (ABA). There are also other compounds that have important growth-regulating activity and function as phytohormones. These include brassinosteroids, jasmonic acid (JA), and salicylic acid (SA). Nitric oxide (NO) is considered a new member of this group [14]. It interacts with other signaling molecules to regulate physiological and molecular processes under optimal and stressful environments. NO plays an important role in resistance to abiotic stresses such as salt, drought, temperature (high and low), UV-B, and heavy metal stress by its antioxidant properties and also by acting as a signal in inducing the activity of ROS-scavenging enzymes to alleviate oxidative stress [15]. It is involved in plant resistance reactions against biotic stresses and

potentiates the induction of hypersensitive cell death in soybean cells by reactive oxygen intermediates. It functions independently of such intermediates to induce genes for the synthesis of protective natural products [16] and enhances adaptive responses to drought stress by inducing stomatal closure [17]. NO mediates ABA-induced stomatal closure via regulation of Ca^{2+} fluxes [18], and closely cooperates with JA, SA, and ethylene in cell responses to different stressors in a complex network [19]. NO functions as a signaling molecule and influences several morphological processes, such as seed germination, root formation, and de-etiolation, and physiological processes through increases in superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) antioxidant enzymes in *Lupinus luteus* [20]. Zheng et al. [21] reported that NO provides signals for salt tolerance by increasing the activity of SOD and CAT, decreasing lipid peroxidation and O_2^- generation rate in the mitochondria.

Independently conducted studies of the roles of NO and S have shown their involvement in salt stress tolerance by interaction with other signaling molecules. There could be interplay between NO and S assimilation in salt tolerance. The present review explains the action of NO and S in salt resistance and describes the potential interplay between NO and S assimilation in salt tolerance.

2. Nitric oxide: Its role in salt tolerance

NO was recognized during the last decade of the 20th century as a signaling molecule with multifaceted physiological roles in plants [22]. It is converted to one of three different species: the radical (NO), the nitrosonium cation, or the nitroxyl anion, showing high reactivity and tendency to bind with reduced heme proteins [23]. Exogenous NO donors constitute a powerful way to supplement plants with NO. Most of the NO donors are organic compounds that form NO complexes such as sodium nitroprusside (SNP) [24]. SNP is the most widely studied compound of the iron nitrosyl family. Studies of Velikova et al. [25] and Courtois et al. [26] have shown a cytoprotective role of NO in photosynthesis by action as an antioxidant molecule or by regulation of stomatal closure and interaction with Ca^{2+} signals. Exogenous application of NO protected cells from oxidative damage under stress by enhancing antioxidant enzymes [27]. Plants emit NO from leaves and herbicide or NO_2 treatment enhances the release of NO [28]. *In vivo* nitrate reductase (NR) assays release NO [29]. Plant mitochondria also make NO from nitrite [30]. However, NO synthesis in plants appears more complex. Major sites of NO biosynthesis in plants are protoplasts, chloroplasts, mitochondria, and peroxisomes [31]. Fig. 1 shows different sources of NO biosynthesis in plants.

The relationship of *Arabidopsis thaliana* NITRIC OXIDE SYNTHASE 1 (AtNOS1) with NOS is debatable. It was previously recognized as a potential NO synthase (NOS) in *A. thaliana* and was shown to be involved in plant development and phytohormones action [32]. Based on similarity to a hypothetical snail NOS or NOS partner that cross-reacted with mammalian NOS antibody, potential NOS was identified in *A. thaliana* [32,33]. Upon knockout of the AtNOS1 gene in *A. thaliana*, reductions in root NO accumulation and NOS activity in leaf extracts were observed. Further, overexpression of AtNOS1 resulted in higher levels of NOS activity in leaf extracts. However, study of

recombinant AtNOS1 revealed no production of the originally reported NOS activity [33]. Recent reports confirm that AtNOS1 is not a NOS and accordingly, it has been renamed NITRIC OXIDE ASSOCIATED PROTEIN1 (AtNOA1). It is now recognized to be a member of the circularly permuted GTPase family (cGTPase) [34,35]. Moreau et al. [35] reported that AtNOS1 was unable to bind and oxidize arginine to NO but specifically bound and hydrolyzed GTP. GTPase activity was necessary but not sufficient for its function in *planta*. cGTPases appeared to be RNA-binding proteins, and the closest homolog of AtNOA1, the *Bacillus subtilis* YqeH, and was shown to participate in ribosome assembly/stability. Moreover, YqeH and AtNOA1 act as G-proteins that regulate nucleic acid recognition and not as NOS [34]. Zhao et al. [36] reported that AtNOA1 functions in root waving. They reported that AtNOA1 modulated SA-induced root waving by affecting cytosolic Ca^{2+} signaling and the PIN-FORMED2 based polar auxin transport pathway, giving new insight into the mechanisms that control root growth behavior. In *Nicotiana benthamiana*, gain-of-function and loss-of-function studies showed that mitogen-activated protein kinase (MAPK) cascade MEK2-SIPK/NTF4 controls NO and ROS generation induced by elicitor INF1, with the latter also modulated by the MEK1-NTF6 cascade [30]. MPK6, the *A. thaliana* ortholog of SIPK, interacts *in vitro* and *in vivo* with NIA2 and phosphorylates NIA2 at a specific serine residue, leading to an increase in NR activity and NO biosynthesis in response to H_2O_2 during *A. thaliana* root development [37].

The protective functions of NO under stressful environments have received attention in recent years. Several studies have shown the protective role of NO in salt-induced damage. The application of $50 \mu\text{mol L}^{-1}$ SNP stimulated ROS-scavenging enzymes and reduced accumulation of H_2O_2 induced by NaCl in mitochondria of *Cucumis sativus* roots [38]. NO serves as a signal in inducing salt resistance by increasing the K^+ to Na^+ ratio, which is dependent on increased PM H^+ -ATPase activity in *Phragmites communis* [39]. The lower concentration of 0.2 mmol L^{-1} SNP was more effective in increasing CAT and glutathione reductase (GR) activity, whereas the higher concentration of 1 mmol L^{-1} SNP was more effective in increasing SOD activity and decreasing membrane injury and lipid peroxidation levels under salt-stress conditions in *Cicer arietinum* [40]. A protective effect of NO on relative water content under salt stress has been reported in *Zea mays* leaves by increase in the activity of vacuolar H^+ -ATPase and H^+ -PPase, which provide the driving force for Na^+/H^+ exchange [41]. Exogenous NO application markedly decreased membrane permeability, rate of O_2 production, contents of MDA and H_2O_2 , and intercellular CO_2 concentration under 50 mmol L^{-1} NaCl stress by increasing the activities of SOD, POD, CAT, and

ascorbate peroxidase (APX), and the contents of photosynthetic pigments and proline [42]. The study of Lopez-Carrion et al. [43] focused on the possible relationship between NO and the induction of proline in response to salt stress and suggested that NO could mitigate the damage associated with salt stress. NO confers salt tolerance on *Kosteletzkya virginica* by preventing both oxidative membrane damage and translocation of Na^+ from roots to shoots [44]. NO produced under salt stress served as a second messenger for the induction of PM H^+ -ATPase expression [39]. NO effectively protected seedlings against salt stress damage by enhancing activity of antioxidant enzymes to quench excess ROS caused by salt stress and promoting the increase of ferritin accumulation to chelate larger numbers of ferrous ions [45]. Exogenous application of NO to salt-grown plants reduced lipid peroxidation and ROS accumulation. Salinity-inhibited growth, measured as reduced leaf area and dry weight, was restored by NO in *Zea mays* [41] and *Oryza sativa* [46]. Pretreatment with NO effectively contributed to better balance between carbon and N metabolism by increasing total soluble protein and enhancing the activity of endopeptidase and carboxypeptidase in plants under salt stress [47]. Zhang et al. [48] reported that NO enhanced salt tolerance in *Populus euphratica* callus under salinity by increasing the K^+/Na^+ ratio, where H_2O_2 was involved in the increase of (PM) H^+ -ATPase activity. Liu et al. [49] showed that the glucose-6-phosphate dehydrogenase enzyme played an important role in NR-dependent NO production and in establishing tolerance of *Phaseolus vulgaris* roots to salt stress. Ruan et al. [50] reported that NO stimulated proline accumulation under salt stress, owing to NO-induced increase in K^+ in *Triticum aestivum* seedling roots under salt stress conditions. Several morpho-physiological parameters, growth, biomass attributes, photosynthetic rate, photosystem II activity, and gas exchange characteristics decreased under salt stress. NO alleviated the decrease of photosynthetic rate induced by non-stomatal factors and damage by photoinhibition to the photosynthetic system. Corpas et al. [51] suggested that adding appropriate SNP alleviated salt toxicity and improved net photosynthesis in *Pisum sativum*. Important studies describing the action of NO in salt tolerance are listed in Table 1, and Fig. 2 shows the mechanisms of NO action in salt tolerance involving various processes in plant cells.

3. S assimilation: Its role in salt tolerance

The management of mineral nutrients plays a key role in augmenting the growth and development of economically important crop plants under varied environmental conditions

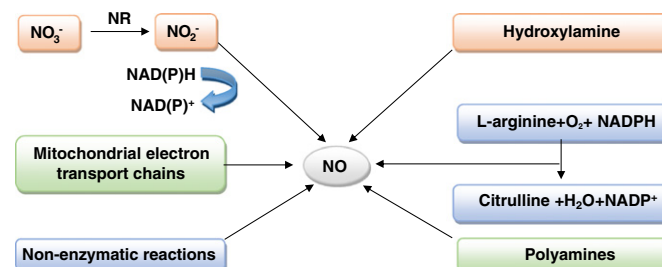


Fig. 1 – Sources of nitric oxide (NO) synthesis in plants.

Table 1 – Studies showing response of plants to NO under salt stress.

Plant	Concentration	Response to nitric oxide	Reference
<i>Lupinus luteus</i>	0.2 mol L ⁻¹ NaCl	Alleviated oxidative stress	[20]
<i>Triticum aestivum</i>	300 mmol L ⁻¹ NaCl	Modulation of ROS and enhances the antioxidant defense system	[21]
<i>Cucumis sativus</i>	100 mmol L ⁻¹ NaCl	Stimulated ROS-scavenging enzymes and reduced accumulation of H ₂ O ₂ in mitochondria of cucumber roots	[38]
<i>Phragmites communis</i>	200 mmol L ⁻¹ NaCl	Increased K ⁺ /Na ⁺ ratio in cytosol	[39]
<i>Zea mays</i>	100 mmol L ⁻¹ NaCl	Increased dry weight	[41]
<i>Cucumis sativus</i>	50 mmol L ⁻¹ NaCl	Enhanced photosynthesis by inducing the photosynthetic pigments	[42]
<i>Brassica rapa</i>	100 mmol L ⁻¹ NaCl	Lowered oxidative stress and proline accumulation	[43]
<i>Kosteletzkyia virginica</i>	100 mmol L ⁻¹ , 200 mmol L ⁻¹ , 300 mmol L ⁻¹ , 400 mmol L ⁻¹	Prevent both oxidative membrane damage and translocation of Na ⁺ from root to shoots	[44]
<i>Oryza sativa</i>	100 mmol L ⁻¹ NaCl	Alleviated oxidative stress	[46]
<i>Suaeda salsa</i>	600 mmol L ⁻¹ NaCl	Enhanced seedlings' growth	[47]
<i>Populus euphratica</i>	150 mmol L ⁻¹ NaCl	Increasing K ⁺ /Na ⁺ ratio in cytosol	[48]
<i>Phaseolus vulgaris</i>	100 mmol L ⁻¹ NaCl	Glucose-6-phosphate dehydrogenase enzyme played an important role in NR-dependant NO production and tolerance of roots to salt stress	[49]
<i>Triticum aestivum</i>	150 and 300 mmol L ⁻¹ NaCl	Enhanced photosynthesis by inducing the photosynthetic pigments	[50]
<i>Zea mays</i>	40 mmol L ⁻¹ NaCl	Contents of N, Na, Cl, Na, K, Ca, Mg, Fe, Zn, and Mn increased by increasing SNP levels	[52]
<i>Arabidopsis thaliana</i>	100 mmol L ⁻¹ NaCl	NO is involved in salt-mediated inhibition of root meristem growth	[53]
<i>Solanum lycopersicum</i>	120 mmol L ⁻¹ NaCl	Increased activity of antioxidant enzymes and enzymes of nitrogen metabolism (NR, NiR)	[54]
<i>Gossypium hirsutum</i>	100 mmol L ⁻¹ NaCl	Increased growth rate and photosynthesis	[55]
<i>Aegiceras corniculatum</i>	350 mmol L ⁻¹ NaCl	Alleviated oxidative damages in leaves	[56]
<i>Cucumis sativus</i>	50 mmol L ⁻¹ NaCl	Enhanced salt tolerance by regulating the content and proportions of the different types of free polyamines	[57]
<i>Zea mays</i>	150 mmol L ⁻¹ NaCl	Reduced salt stress-induced oxidative stress and caspase-like activity via enhanced antioxidant enzyme activity	[58]
<i>Triticum aestivum</i>	150 and 300 mmol L ⁻¹ NaCl	Modulation of antioxidant defense system	[59]
<i>Triticum aestivum</i>		Increased total soluble protein and by enhancing the activities of endopeptidase and carboxypeptidase	[60]
<i>Cicer arietinum</i>	100 mmol L ⁻¹ NaCl	Positive effect on antioxidant enzymes (CAT, POX, APX)	[61]
<i>Triticum aestivum</i>	100 mmol L ⁻¹ NaCl	Stimulated PM H ⁺ -ATPase activity to modulate ion homeostasis for salt tolerance	[62]
<i>Triticum aestivum</i>	150 mmol L ⁻¹	Enhanced H ⁺ -ATPase and H ⁺ -PPase, but did not affect the H ⁺ transport ability across plasma membrane	[62]

[63,64]. Supplementation with S has significant role in protection against salt-induced oxidative damage [9]. Enzymes of the S-assimilatory pathway were induced by application of S under salt stress and helped in neutralizing or scavenging ROS [5,7–10].

S assimilation is highly regulated in a demand-driven manner [6,9,10,65,66]. S is taken up by roots in the form of sulfate. The uptake of sulfate by roots and transport to shoot are strictly controlled and appear as primary points of regulation of S assimilation. Sulfate reduction takes place in leaf chloroplasts and produces sulfide. The key regulatory steps of sulfate assimilation are the activation of sulfate in cells by ATP-sulfurylase (ATPS) and the reduction of adenosine 5'-phosphosulfate (APS) to sulfite by APS reductase (APR) [67]. Sulfite is reduced by sulfite reductase with ferredoxin as a reductant and the sulfide formed is further incorporated into Cys by coupling to O-acetyl serine (OAS). The process is controlled by the enzyme OAS thiol lyase, also called Cys synthase. Cys is used for the production of GSH.

GSH is an important S-containing compound associated with the exclusion of ROS [4]. The S-containing group thiol is strongly nucleophilic and suitable for biological redox reactions and plays

an important role in protection against salt stress-induced oxidative damage [9]. Astolfi et al. [68] reported that salt-stress affected root thiol content through its effects on the rate of S assimilation. External S supply improves salinity tolerance by meeting the demand for GSH synthesis via increased Cys synthesis [9]. Plants grown with salt showed increased S assimilation, resulting in higher Cys biosynthesis required for increased GSH production and defense responses to salt stress [69–72]. Thus, the regulation of synthesis of S-containing compounds using genetic tools offers potential option for increasing salt tolerance. The upregulation of Cys synthesis in *A. thaliana* in response to salt stress [73] augments GSH content, which in turn plays a protective role against salt stress in the plant. In addition, transgenic approaches have been employed successfully to increase the capacity of salt tolerance in plants by manipulation of S assimilation and metabolism. In plants, S-containing compounds such as methionine, thioredoxins, vitamins, and coenzyme A play an important role in salt stress responses in addition to Cys and GSH [72]. Methionine acts as a regulatory molecule as part of S-adenosyl methionine (SAM). The level of SAM synthase increases significantly under salt stress, suggesting the sensitivity of the methionine pathway

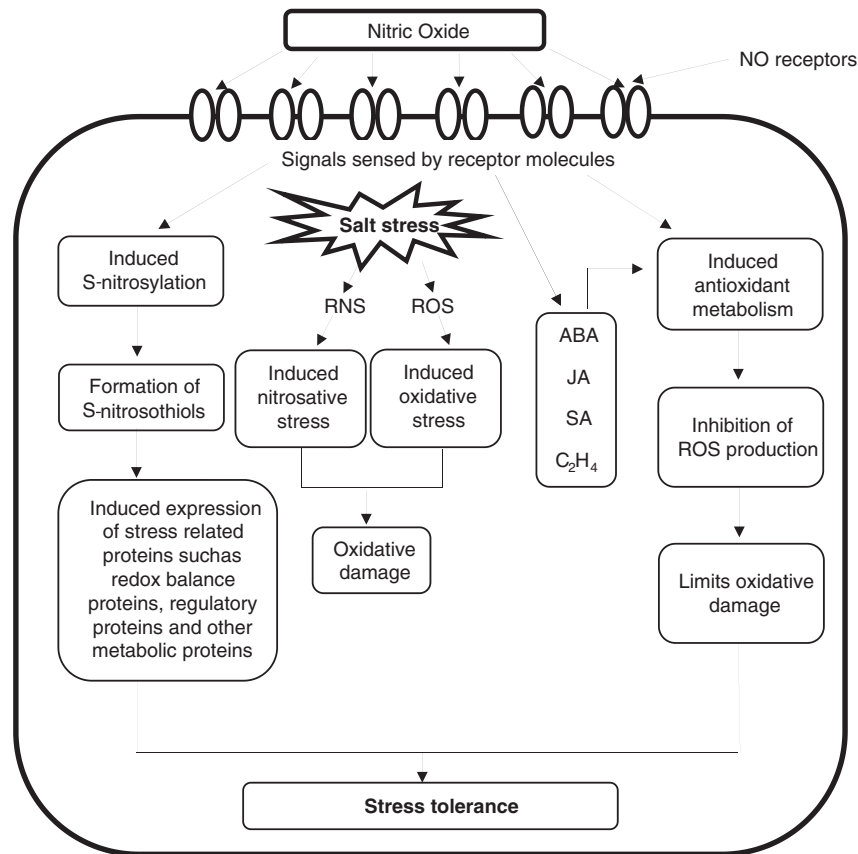


Fig. 2 – Nitric oxide signaling in plant cells under stressful environments. Salt stress induces reactive nitrogen species (RNS) and reactive oxygen species (ROS) and causes oxidative damage in plant cells. NO induces S-nitrosylation and formation of nitrosothiols, thereby inducing the expression of stress-associated proteins. NO also influences the antioxidant system and increases the activity of antioxidant enzymes that subsequently inhibit ROS generation and limit oxidative damage. NO influences signaling of abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA), and ethylene under stress. These phytohormones induce antioxidant system in plants resulting in induced stress tolerance.

to salt stress, and its supplementation has been reported to increase salt tolerance [5,72]. Thioredoxins are small (12–13 kDa) ubiquitous, heat-stable proteins involved in responses of plants to salt stress [5]. They participate in ROS metabolism and reduce H_2O_2 production by acting as a hydrogen donor and signal for plant salt stress responses [4,72]. El-Shintinawy et al. [74] reported that the addition of thiamine to medium alleviated salt stress by increasing the contents of Cys and methionine. Table 2 lists studies of the role of S assimilation in salt tolerance.

4. Interplay between NO and S assimilation in regulation of salt tolerance

Coordination between phytohormones and nutritional signaling plays an important role in salt tolerance. Phytohormones such as JA, ABA, SA, and ethylene play important roles in the accumulation of GSH under stressful conditions [66]. Phytohormones such as ethylene and SA affect salt tolerance by regulating S metabolism [8,85,86]. Moreover, the interaction between ROS and the AsA-GSH cycle triggers the synthesis of JA and SA [87], which

further help in the upregulation of nutrient uptake under nutrient deficit conditions. It has been suggested that NO is involved in reducing oxidative stress through GSH formation under salt stress [88]. Supplementation with S-regulated GSH content in plants through induced S assimilation [10]. Thus, there is a possibility of interaction between NO and S assimilation. Barroso et al. [89] showed that both NO and NO-derived peroxynitrite react with GSH to generate S-nitrosoglutathione (GSNO), which behaves as an NO donor in plant tissues. The enzyme GSNO reductase (GSNOR) involved in the formation of GSNO played an important role in alleviating and limiting NO in plant cells under stress conditions [89,90]. The reduction of the metabolite GSNO to oxidized glutathione (GSSG) and NH_3 is catalyzed by GSNOR. The resulting GSSG is then reduced again to GSH in an NADPH-dependent reaction catalyzed by GR [14]. Figure 3 shows that application of both NO and S reduces NaCl-induced oxidative stress by regulating NO generation in plants receiving S. An improvement in GSH content and redox state resulted in enhanced salt tolerance through an increase in the antioxidant system and efficiency of AsA-GSH cycle [91]. NO triggers expression of redox-regulated defense-associated genes directly or indirectly to establish stress tolerance [92].

Table 2 – Studies showing response of some plants to S assimilation under salt stress.

Plant name	Salt stress	Response	Reference
<i>Brassica juncea</i>	50, 100 mmol L ⁻¹ NaCl	Increase in ATP-S activity	[71]
<i>Arabidopsis thaliana</i>	0.17 mol L ⁻¹ NaCl	Increase in cysteine content	[73]
<i>Hordeum vulgare</i>	100 mmol L ⁻¹ NaCl	Increase in GSH synthesis, avoids the effects of ROS on photosynthetic functions	[75]
<i>Triticum aestivum</i>	100 mmol L ⁻¹ NaCl	Increase in GSH content	[76]
<i>Vigna radiata</i>	50 mmol L ⁻¹ NaCl	Sulfur assimilation enhanced salt tolerance	[77]
<i>Populus × canescens</i>	75 mmol L ⁻¹ NaCl	Increase in GSH concentration protected PS II damage	[78]
<i>Pyrus betulaefolia</i>	150 and 200 mmol L ⁻¹ NaCl	Stimulated accumulation of GSH	[79]
<i>Phyllanthus amarus</i>	80 mmol L ⁻¹	Decrease in GSH content	[80]
<i>Typha latifolia</i> , <i>Phragmites australis</i>	100 mmol L ⁻¹ NaCl	Increase in cysteine content	[81]
<i>Gossypium</i> spp.	50, 100, and 200 mmol L ⁻¹ NaCl	Increase in GR activity	[82]
<i>Lycopersicon esculentum</i>	100 mmol L ⁻¹ NaCl	Increased GSH content and GSH:GSSG (oxidized glutathione)	[83]
<i>Lycopersicon pennellii</i>	100 mmol L ⁻¹ NaCl	Increase in GSH content	[84]

NO enhances the activity of SOD and CAT, which separately contribute to a delay in H₂O₂ accumulation and elevate the proportions of GSH/GSSG and AsA/DHA in *T. aestivum* leaves to protect from oxidative damage caused by salt stress [93]. Plants with impaired GSNO metabolism are compromised in several physiological processes. Both GSNO and GSNOR were downregulated under cadmium stress in *P. sativum* [89], indicating that fine control of S-nitrothiol homeostasis was important for growth, development, and resistance to abiotic stresses [94]. However, the peroxynitrite formed from the reaction of NO with ROS has been found to be one of the major cell antioxidants that are important in the control of ROS metabolism. Baudouin and Hancock [95] summarized GSNO

metabolism and suggested the occurrence and function of GSNO in plant cells, along with other NO reaction products. These are important issues for future understanding of the role of NO in plant development and stress responses. Sehwat et al. [96] suggested that the depletion of Rubisco from samples improved proteome coverage of cold-responsive S-nitrosylated targets in *Brassica juncea*. Recently, it has been proposed that NO negatively regulates CK signaling by limiting phosphorelay activity via S-nitrosylation [97]. NO also activates different biochemical pathways and interacts with metals to produce metal proteins, and with sulfhydryl groups and nitro groups in the process of nitration to provide resistance against salt stress [14,98].

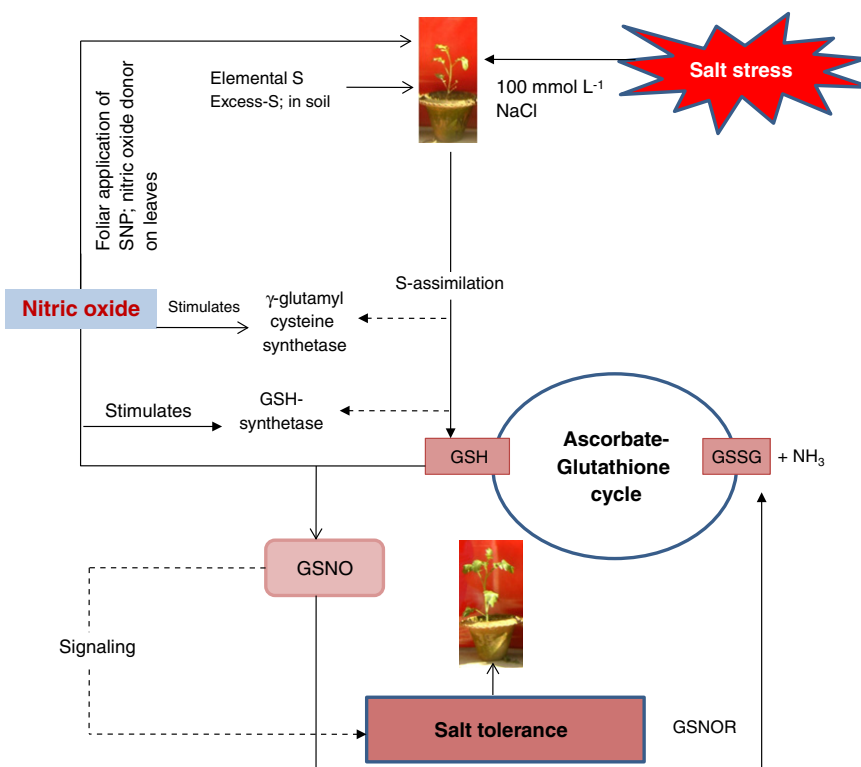


Fig. 3 – Schematic representation showing the alleviation of salt stress in plants via excess S and nitric oxide-dependent responses involving the ascorbate–glutathione system.

5. Conclusion and future prospects

NO plays an important role in tolerance to salt stress in plants. It acts as a signal molecule and induces salt tolerance in plants by enhancing S assimilation and synthesis of S compounds and modulating the activity of antioxidant enzymes. Interaction between NO and S assimilation regulates GSH synthesis for the adaptation of plants to stressful environments. The regulatory interaction between NO and S can be manipulated for adjusting plants to the changing environment for sustainable agricultural development. However, studies are needed to trace the signaling pathways of NO action and its biosynthesis in response to environmental cues. Moreover, the physiological and molecular mechanisms by which NO induces S assimilation, and how it interacts with other plant hormones and nutrients to achieve plant salt tolerance, await investigation.

Acknowledgments

INSPIRE Fellowship to the first author by the Department of Science & Technology, New Delhi and research facilities in lab of NAK in the DBT-BUILDER programme (No. BT/PR4872/INF/22/150/2012) of Department of Biotechnology, New Delhi, are gratefully acknowledged.

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