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REVIEW

# Nitric oxide-induced salt stress tolerance in plants: ROS metabolism, signaling, and molecular interactions

**Mirza Hasanuzzaman**[1,2] · **Hirosuke Oku**[1] · **Kamrun Nahar**[3] · **M. H. M. Borhannuddin Bhuyan**[4] · **Jubayer Al Mahmud**[5] · **Frantisek Baluska**[6] · **Masayuki Fujita**[4]

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## Abstract

Nitric oxide (NO), a non-charged, small, gaseous free-radical, is a signaling molecule in all plant cells. Several studies have proposed multifarious physiological roles for NO, from seed germination to plant maturation and senescence. Nitric oxide is thought to act as an antioxidant, quenching ROS during oxidative stress and reducing lipid peroxidation. NO also mediates photosynthesis and stomatal conductance and regulates programmed cell death, thus providing tolerance to abiotic stress. In mitochondria, NO participates in the electron transport pathway. Nitric oxide synthase and nitrate reductase are the key enzymes involved in NO-biosynthesis in aerobic plants, but non-enzymatic pathways have been reported as well. Nitric oxide can interact with a broad range of molecules, leading to the modification of protein activity, GSH biosynthesis, *S*-nitrosylation, peroxynitrite formation, proline accumulation, etc., to sustain stress tolerance. In addition to these interactions, NO interacts with fatty acids to form nitro-fatty acids as signals for antioxidant defense. Polyamines and NO interact positively to increase polyamine content and activity. A large number of genes are reprogrammed by NO; among these genes, proline metabolism genes are upregulated. Exogenous NO application is also shown to be involved in salinity tolerance and/or resistance via growth promotion, reversing oxidative damage and maintaining ion homeostasis. This review highlights NO-mediated salinity-stress tolerance in plants, including NO biosynthesis, regulation, and signaling. Nitric oxide-mediated ROS metabolism, antioxidant defense, and gene expression and the interactions of NO with other bioactive molecules are also discussed. We conclude the review with a discussion of unsolved issues and suggestions for future research.

**Keywords** Abiotic stress · Antioxidant defense · Glutathione · Hydrogen sulfide · Polyamines · Stress tolerance

## Abbreviations

| | |
|---|---|
| ABA | Abscisic acid |
| APX | Ascorbate peroxidase |
| AsA | Ascorbate |
| ATP | Adenosine triphosphate |
| CAT | Catalase |
| chl | Chlorophyll |
| DHAR | Dehydroascorbate reductase |
| ETH | Ethylene |
| GPX | Glutathione peroxidase |

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✉ Masayuki Fujita
fujita@ag.kagawa-u.ac.jp

Mirza Hasanuzzaman
mhzsauag@yahoo.com

[1] Molecular Biotechnology Group, Center of Molecular Biosciences, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213, Japan

[2] Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka 1207, Bangladesh

[3] Department of Agricultural Botany, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka 1207, Bangladesh

[4] Laboratory of Plant Stress Responses, Faculty of Agriculture, Kagawa University, Miki-cho, Kita-gun, Takamatsu, Kagawa 761-0795, Japan

[5] Department of Agroforestry and Environment, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Dhaka 1207, Bangladesh

[6] Department of Plant Cell Biology, Institute of Cellular and Molecular Botany (IZMB), University of Bonn, Kirschallee 1, 53115 Bonn, Germany

| | |
|---|---|
| GSH | Glutathione |
| GR | Glutathione reductase |
| GSNO | *S*-Nitrosoglutathione |
| GSNOR | GSNO reductase |
| GST | Glutathione *S*-transferase |
| $H_2S$ | Hydrogen sulfide |
| MAPK | Mitogen-activated protein kinase |
| MDA | Malondialdehyde |
| MDHAR | Monodehydroascorbate reductase |
| MG | Methylglyoxal |
| $NO_2$-FAs | Nitro-fatty acids |
| NO | Nitric oxide |
| NOS | NO synthase |
| NR | Nitrate reductase |
| PA | Polyamine |
| PCD | Programmed cell death |
| PM | Plasma membrane |
| POD | Guiacol peroxidase |
| PTM | Post-translational modification |
| ROS | Reactive oxygen species |
| RNS | Reactive nitrogen species |
| RuBisCO | Ribulose-1,5-bisphosphate carboxylase/oxygenase |
| SNAP | *S*-Nitroso-*N*-acetylpenicillamine |
| SNP | Sodium nitroprusside |
| SOD | Superoxide dismutase |
| XOR | Xanthine oxidoreductase |

## Introduction

Worldwide, approximately 930 million hectares of arable land, representing more than 6% of the world's total land area, are subjected to salt stress, and this percentage is increasing daily with climate change due to natural and anthropogenic activity (Munns and Tester 2008; Setia et al. 2013). At the physiological level, salt stress triggers osmotic stress and ionic stress. Salt-induced osmotic stress interrupts plant–water relations and hampers cell expansion and division. Due to ionic toxicity, nutrient homeostasis is disrupted, which leads to other stress factors associated with cellular functioning. Thus, plants under salt stress are affected in germination, growth, and developmental stages. Plant productivity with respect to biological or reproductive yield is diminished significantly under salt stress. Severe salt stress can cause plant death (Munns and Tester 2008). In a salty environment, plants cannot take up water due to osmotic stress; the dehydration stress perturbs stomatal conductance and the functioning of photosynthetic enzymes. This anomalous behavior leads to exacerbated ionic toxicity and nutrient imbalance in salt-affected plants. These physiological alterations lead to overproduction of reactive oxygen species (ROS), which severely damage cell membranes and other cellular components via oxidation of proteins and peroxidation of lipids. Nuclear material carrying genetic information, i.e., DNA, can be structurally altered due to this oxidative stress. Thus, oxidative stress has severe adverse effects in salt-affected plants (Hasanuzzaman et al. 2013a, b, c). Plants with antioxidant defense systems can combat ROS generation to an extent. This strategy is a good defense under normal growth conditions, but under conditions of stress, including salt stress, ROS are overproduced and cannot be overcome by the antioxidant defense system of the plant. Plants that can enhance the antioxidant defense system under conditions of stress are tolerant to ROS (Munns and Tester 2008; Hasanuzzaman et al. 2013a, b; Ahmad et al. 2016).

Nitric oxide (NO) is a gaseous, free-radical, redox-signaling molecule with diverse functions. NO acts as a messenger in various physiological processes and has been reported to affect plant responses to salt stress, excess light, low temperatures, high temperatures, ozone, UV-B, toxic-metal stress and various pathogens (Gaupels et al. 2011; Hasanuzzaman et al. 2012; Gill et al. 2013; Mur et al. 2013; Nahar et al. 2016). In salt-affected plants, seed vigor and germination are improved by NO (Hayat et al. 2012). Nitric oxide alleviates oxidative damage, improves the antioxidant defense mechanism, decreases methylglyoxal toxicity, and upregulates the glyoxalase system in salt-affected wheat plants (Hasanuzzaman et al. 2011). By adjusting the levels of osmolytes and antioxidant enzymes, NO alleviated salt-induced damage in chickpea plants (Ahmad et al. 2016). In salt-affected Bermuda grass, sodium nitroprusside (SNP, an NO donor) assuaged the damaging effects of NO on plant growth, ionic balance ($K^+$:$Na^+$, $Mg^{2+}$:$Na^+$, and $Ca^{2+}$:$Na^+$ ratios), water content, and chlorophyll (chl) content, and higher chl *a* fluorescence curves were observed. Additionally, decreased levels of electrolyte leakage, malondialdehyde (MDA), and hydrogen peroxide ($H_2O_2$) and improved antioxidant enzyme activities were observed (Liu et al. 2016).

Nitric oxide rapidly reacts and interacts with other radicals/ROS, phytohormones, and signaling molecules. NO can react with pro- and antioxidants (Hill et al. 2010). There is cross-talk between NO and other molecules that regulate vital physiological processes. Calcium (Ca)-calmodulin and NO in abscisic acid (ABA) and $H_2O_2$ signaling modulate antioxidant defense components in maize leaves (Sang et al. 2008). Interactions between ABA, $H_2O_2$, NO, and mitogen-activated protein kinase (MAPK)- induced stomatal closure and antioxidant defense in plants for survival under conditions of water stress (Hao and Zhang 2010). *S*-Nitrosoglutathione (GSNO), which is generated by the *S*-nitrosylation reaction of NO with glutathione, plays regulatory roles in the maintenance of the trans-nitrosation equilibrium between GSNO and *S*-nitrosylated proteins (Cheng et al. 2017). GSNO reductase (GSNOR) plays a regulatory role in post-translational modifications of cysteine residues (Tichá et al.

2017). GSNOR participates in activation of the antioxidant system, regulation of ROS and reactive nitrogen species (RNS) generation, the cellular redox status, stimulation of stress-responsive genes, and stress-induced programmed cell death (PCD) (Cheng et al. 2017; Tichá et al. 2017). All these features make NO a powerful molecule, the diverse roles of which are revealed daily in this era of complex environmental stress. In this review, NO-induced modulation of ROS metabolism and the signaling role and molecular interactions of NO with other molecules are discussed with respect to the development of salt tolerance in plants.

## Salt stress in plants: a brief overview

Salinity is one of the most devastating abiotic stress factors in agriculture worldwide and is anticipated to be drastically enhanced by global climate change (da Silva et al. 2017; Reddy et al. 2017). Nearly 7% of the land in the world has high salt content, and approximately 20% of the cultivated land and 33% of the irrigated land area in the world are salt-affected and degraded (Kibria et al. 2017, Machado and; Serralheiro et al. 2017). Moreover, roughly three hectares of arable land is affected by soil salinization per minute, which leads to a 10% increase in salinity-affected area annually (Shrivastava and Kumar 2015; Bose et al. 2017). The most common soluble salts in soil are sodium chloride (NaCl) and sodium sulfate ($Na_2SO_4$). In addition, soil contains a considerable amount of calcium sulfate ($CaSO_4$), magnesium sulfate ($MgSO_4$), potassium nitrate ($KNO_3$), sodium bicarbonate ($NaHCO_3$), etc. However, most of these salts are not fully soluble in water (Hasanuzzaman et al. 2013a). Therefore, most widespread causes of soil salinity are $Na^+$ and $Cl^-$ ions. Physiologically, salinity is considered one of the most limiting factors for plant growth and development due to the multifarious negative effects of salinity, including specific ion toxicity, osmotic stress, and oxidative damage in plants (Munns et al. 2006; Bose et al. 2017). Ion toxicity occurs due to disequilibrium in ion homeostasis. Salt in plant growth medium increases the $Na^+$ levels, which competes with $K^+$ uptake. Therefore, $Na^+$ uptake increases, which causes $K^+$ efflux and triggers $K^+$ leakage from plant cells, ultimately resulting in $K^+$ deficiency in the cytosol (Chokshi et al. 2017). Furthermore, $Na^+$ replaces $Ca^{2+}$ from the cell membrane, which also enhances the intracellular $Na^+$ content. Consequently, during salinization, the $Na^+$ content destroys the nutrient balance, particularly the $Na^+/K^+$ ratio (Rahman et al. 2016). The incidence of high salinity in soil or in any plant-growth medium decreases the osmotic potential, which reduces water uptake and even forces water out of the cell, resulting in closure of the stomata (Shabala and Cuin 2007; Chokshi et al. 2017; Rajput et al. 2017). Both ion toxicity and osmotic stress ultimately hinder the plant photosystem and lead to excess ROS and methylglyoxal (MG) production (Hasanuzzaman et al. 2017a). In addition to overproduction of ROS [singlet oxygens ($^1O_2$), superoxide anions ($O_2^{\bullet -}$), $H_2O_2$, and hydroxyl radicals (OH•)] and MG in a plant cell, salt-stress perturbs the antioxidant defense and glyoxalase system, which leads to oxidative stress (Hasanuzzaman et al. 2013a, 2017a). On the other hand, $Cl^-$ is more dangerous than $Na^+$ and causes many physiological disorders in plants. In addition to destroying nutrient balance, $Cl^-$ can induce chlorotic toxicity symptoms in plants due to impaired production of chl (Tavakkoli et al. 2010; Hasanuzzaman et al. 2013a).

Overall, major physiological and biochemical processes of plants, including photosynthesis, protein synthesis, and respiration, are perturbed upon the initiation of salt stress, which ultimately leads to growth inhibition or death of the plant (Fig. 1; Rahman et al. 2017). Germination, the most important phase of the plant life cycle, is severely hampered by salt stress (Hasanuzzaman et al. 2013a). Important processes involved in germination, such as imbibition, activation of different metabolic pathways, emergence of embryonic tissue, and seedling establishment, are severely affected by salinity (Hasanuzzaman et al. 2013b; Ibrahim 2016; Rahman et al. 2017). Rahman et al. (2016) experimented with rice plants and observed that salt stress caused water shortage and chlorosis in the plant, which ultimately reduced plant growth. They also reported that salt-induced stress perturbed ion homeostasis via $Na^+$ influx and $K^+$ efflux. Moreover, salt-induced stress reduced the uptake of different nutrients that were essential for the plant. Increased

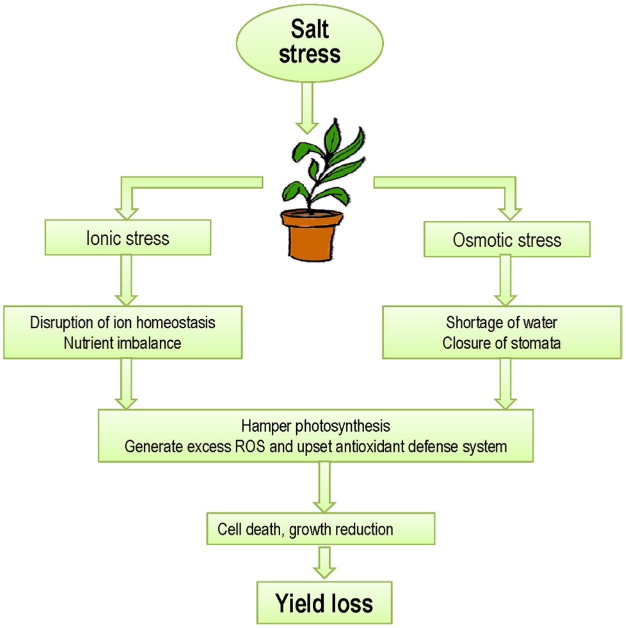


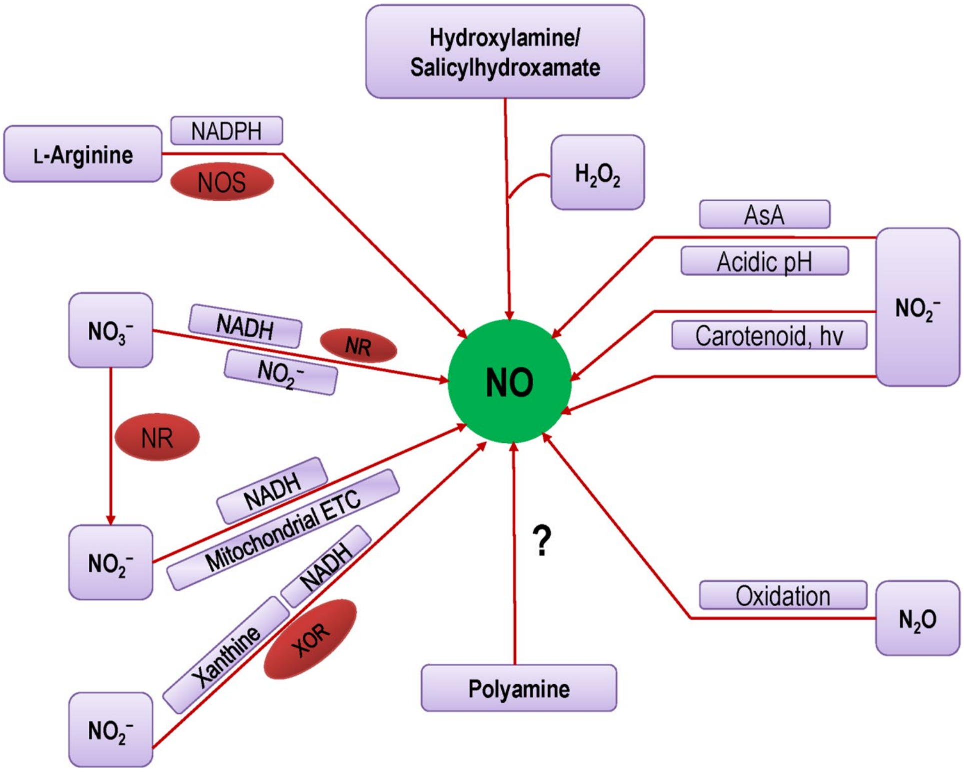
**Fig. 1** Consequence of salt-induced stress in plants

lipid peroxidation and loss of plasma membrane integrity were observed in salt-stressed rice plants due to over-generation of ROS and MG along with alteration of antioxidant defense and glyoxalase systems. Similar growth reductions via salt-induced oxidative stress were observed in many plants by several groups of scientists (Kibria et al. 2017; Chokshi et al. 2017). Salinity not only hinders germination and plant growth, but also reduces the yield and adversely affects yield-associated parameters and grain quality (Rahman et al. 2017; Reddy et al. 2017). Stavridou et al. (2017) observed that the biomass yield of bioenergy grass was notably hampered by salinity. Therefore, it is evident that salt-induced stress greatly hinders the growth and yield of plants by destroying the nutrient status of the plant-growth medium and perturbing the physiology and metabolism of the plant.

## Nitric oxide biosynthesis in plants and its regulation

Since NO research began in animal systems, the biosynthetic pathway of NO in animals is well understood. Research in different plant species at different times has demonstrated various possible pathways of NO biosynthesis. Different researchers have shown NO-biosynthesis pathways in different plant species. There is no common or clear description of NO biosynthesis, which is why, in this review, we have attempted to summarize the information from available literature. An overview of the potential routes of plant NO production has been presented in Fig. 2. The nitrogen cycle represents the atmospheric nitrogen (N) that is incorporated via fixation (fixed by lightning strikes and symbiotic bacteria) and is then assimilated. Following ammonification, nitrification, and denitrification, the N is returned to the environment. Nitrification converts ammonia to nitrites ($NO_2^-$), and nitrites ($NO_2^-$) are oxidized to nitrates ($NO_3^-$) (Ghaly and Ramakrishnan 2015). Nitric oxide production may occur via enzymatic and non-enzymatic pathways. Oxidation of L-arginine via an NADPH-dependent pathway leads to the biosynthesis of NO. Here, NO synthase (NOS) is a catalytic agent (Foresi et al. 2010). Nitrite is converted to nitrate via nitrate reductase (NR) activity, and nitrite is subsequently reduced to NO by NR. Nitrite can be converted to NO via the mitochondrial electron transport chain (Yamasaki et al. 1999; Gupta et al. 2011). Xanthine oxidoreductase (XOR) has been reported to produce NO from nitrite using xanthine (Harrison 2002). Nitric oxide can be produced from hydroxylamine (HA) or salicylhydroxamate (SHAM). Production of NO was decreased by anoxia or by the addition of catalase (CAT), but was increased by conditions that induced reactive oxygen (ROS) or by the addition of $H_2O_2$. Addition of superoxide dismutase (SOD) stimulates $H_2O_2$ production and ultimately stimulates NO production (Rümer et al. 2009). Reduction of $NO_2$ to NO by carotenoids can occur at low pH in the absence of enzymes (Crawford 2006). Phenolic compounds such as catechin can also reduce $NO_2$ to NO (Bethke

**Fig. 2** Overview of possible routes of NO biosynthesis in plants



et al. 2004). Nitric oxide can be generated from $N_2O$ via oxidation (Schreiber et al. 2012). Polyamines have also been shown to be a source of NO, but the complete pathway has not been elucidated (Tun et al. 2006). When oxygen is available in normal conditions, NO biosynthesis occurs in peroxisomes, chloroplasts, and mitochondria (Wulff et al. 2009; Galatro et al. 2013; Corpas and Barroso 2014). In hypoxic or anoxic conditions, nitrite is reduced to NO by non-symbiotic hemoglobins, deoxy-heme proteins, and molybdo-cofactors or mitochondrial cytochrome c oxidase (Gupta et al. 2011). Further research is required to obtain a clear understanding of the NO biosynthesis pathway.

## Nitric oxide improves plant physiology under salt-induced stress

Nitric oxide plays key roles in various physiological mechanisms required for growth and development of the plants and in biotic and abiotic stress response (Fig. 3; Siddiqui et al. 2011; Hasanuzzaman et al. 2013c, 2017b; Zuccarelli et al. 2017). However, the information available on salt-stress tolerance is controversial to some extent, and salt-stress tolerance is dependent on crop species, seedling age, and duration and severity of stress treatment (Hasanuzzaman et al. 2013c).

Seed priming with NO from exogenous sources, such as SNP, showed a promising effect on the control of germination under NaCl-induced stress. Wheat seeds (*Triticum aestivum* L., cv. Huaimai 17) were reported to have increased germination rates and radical and coleoptile weight under saline conditions (300 mM NaCl) upon treatment with NO (0.1 mM SNP) for 20 h. The seed respiration rate also increased. Furthermore, $K^+$ and $Na^+$ ion homeostasis and degradation of stored starch to yield soluble sugars increased with NO pretreatment (Zheng et al. 2009; Marvasi 2017). Exogenous application of NO has been proven to be advantageous for increasing the dry mass and shoot and root lengths of NaCl-stressed plants (Kausar et al. 2013). Decreased leaf area and decreased plant dry-matter production due to salt stress can be alleviated with NO application in several crops (Fatma and Khan 2014).

**Fig. 3** Role of NO in plants under salt-induced stress

Nitric oxide improves photosynthetic capacity by protecting photosynthetic pigments in leaves. Enhancement of photosynthetic capacity following NO treatment was observed with quenching of additional energy and quantum-yield enhancement of photosystem II (PSII) in *Solanum melongena* (Wu et al. 2013). Under salt-induced stress, NO treatment enhanced the photosynthetic machinery in *B. juncea* (Fatma and Khan 2014). Fatma et al. (2016a) found that under conditions of sufficient sulfur (S) supply, NO improves photosynthesis in salt-stressed *B. juncea* plants. They also reported that NO and S enhance the normal shape of thylakoids and increase chloroplast size, which facilitates higher chl content in salt-stressed plants. In conditions of stress, NO increased the uptake and translocation of several macro- and micronutrients, such as K, Mg, Zn and Fe, which enhance chl biosynthesis and respiration (Wang et al. 2013; Kong et al. 2014; Dong et al. 2015). Additionally, NO affects stomatal regulation. Reports show that exogenous NO increases stomatal conductance and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activity, thereby enhancing photosynthesis under conditions of salt-induced stress (Fatma and Khan 2014). Stomatal conductance is closely associated with the osmotic status of plant cells. Under conditions of salt-induced stress, plants close their stomata to cope with physiological drought. Increased ABA accumulation triggers stomatal closure, while exogenous NO and S induce stomatal opening. Moreover, NO induces the influx and efflux of $Ca^{2+}$, thereby regulating stomatal movement and ABA concentration in guard cells (Wang 2014; Fatma and Khan 2014). Exogenous application of NO has been reported to slow down electron transport and inhibit the process of nonphotochemical and photochemical quenching (Wodala et al. 2008; Wu et al. 2010). Thus, NO helps in efficient energy dissipation.

Nitric oxide was reported to maintain ion homeostasis in plants exposed to saline conditions. NO helps the plants to enhance $K^+$ uptake while reducing $Na^+$ uptake and using a portion of the $Na^+$ surplus to resist against salinity. In this compartmentalization process, the $Na^+/H^+$ antiporter enzyme is involved in the removal of cytosolic $Na^+$ (Chen et al. 2010). Nitric oxide triggers the vacuolar $H^+$-ATPase, and $H^+$-PPase, which forces the $Na^+/H^+$ ion exchange to detoxify the cell. Several researchers have reported increased $H^+$-ATPase activity during $Na^+$ compartmentalization. In *Zea mays*, for example, exogenous NO increased the activity of $H^+$-ATPase, leading to a high $K^+/Na^+$ ratio in the cytosol and inducing high salt tolerance in plants (Zhang et al. 2006). Exogenous use of an NO donor (50 µM SNP) is also a promising strategy allowing plants to cope with salt-induced stress by reducing ion leakage (Marvasi 2017).

## Nitric oxide regulates ROS metabolism and antioxidant defense during salt-induced stress

Nitric oxide can directly or indirectly act on a broad range of targets, leading to the attenuation of oxidative stress by upregulating non-enzymatic and enzymatic antioxidants (Table 1; Fig. 4; Christou et al. 2014; Ahmad et al. 2016; Kong et al. 2016; da Silva et al. 2017). Nitric oxide is also recognized as a secondary antioxidant because NO has antioxidant properties that can counteract abiotic stress-induced ROS either by direct scavenging or by triggering the activity of various ROS-scavenging enzymes (Siddiqui et al. 2011; Hasanuzzaman et al. 2013c; Arora et al. 2016). Furthermore, NO is recognized as a powerful inhibitor of ROS that cause lipid peroxidation and protein oxidation (Fancy et al. 2017). Salt-induced stress increased the endogenous NO content in plants, which prevented salinity-induced damage to a certain extent (Fatma et al. 2016b; da Silva et al. 2017). In fact, in the last few years, exogenous application of NO to induce salt-stress tolerance in different plant species has gained popularity. Fan et al. (2007) carried out an experiment with the *Cucumis sativus* plant under salt-induced stress (50 mM NaCl) in combination with 10–400 µM SNP and found that, in contrast to salt-induced stress, 50 µM SNP enhanced the activity of antioxidant enzymes, including SOD, CAT, guaiacol peroxidase (POD), and ascorbate peroxidase (APX), which helped reduce membrane permeability, MDA content, $H_2O_2$ content and $O_2^{\bullet -}$ generation. subsequently, Sheokand et al. (2008) reported that 0.2 mM SNP increases the APX and peroxidase (POX) activity of salt-stressed *Cicer arietinum*. Accordingly, the MDA content of and relative injury to the plant due to overproduction of ROS were decreased in the presence of NO. At the same time, various reports indicated the protective role of NO in salt-stress tolerance due to the upregulation of antioxidant activity in various plant species, such as *Kosteletzkya virginica* (Guo et al. 2009), *T. aestivum* L. (Zheng et al. 2009), and *C. arietinum* L. (Sheokand et al. 2010). Hasanuzzaman et al. (2011) grew *T. aestivum* in 300 mM NaCl with 1 mM SNP and observed that NO contributed to the upregulation of both enzymatic (monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione reductase, GR; glutathione *S*-transferase, GST; glutathione peroxidase, GPX; and CAT) and non-enzymatic (glutathione, GSH; and ascorbate, AsA) antioxidants. As a result, salt-induced enhancement of MDA and $H_2O_2$ levels decreased significantly. Similar SNP-induced salt-stress tolerance due to the positive effects of NO on the antioxidant defense system and ROS metabolism was observed in *Lycopersicon esculentum* (Wu et al. 2011), *Aegiceras corniculatum* (Chen et al. 2014), *B. juncea* (Gupta et al. 2017) and *P. sativum* (Yadu et al. 2017). Egbichi et al. (2014) used 2,2′(hydroxynitrosohydrazono) bis-ethanimine (DETA) as another NO-generating compound to combat salt-induced stress. When they used 10 µM DETA with 80 mM NaCl, they found that NO helped to increase APX activity, which leads to decreased $H_2O_2$ content. Recently, several types of studies have been conducted by many groups of scientists to confirm the positive role of NO against salt-induced stress. Ahmad et al. (2016) used 50 µM *S*-nitroso-*N*-acetylpenicillamine (SNAP) as a NO source and found that SNAP increased the activities of SOD, CAT, APX, and GR in the *C. arietinum* plant, which reduced the $H_2O_2$ and MDA content and decreased electrolyte leakage. In addition to co- or pretreatment of seedlings, seed priming with NO is also effective against salt-induced stress. Ali et al. (2017) and Gadelha et al. (2017) primed test seeds with 0.1 mM and 75 µM SNP, respectively, and observed positive results against 150 and 100 mM NaCl, respectively. Therefore, both endogenous and exogenous NO (seed priming, pretreatment or cotreatment) can play a positive role in the mitigation of salt-induced oxidative stress to a certain extent, but the effect is dose dependent and varies from plant to plant.

## Nitric oxide signaling under salt-induced stress

Signaling is the conversion of certain stimuli to a series of intracellular events. Signaling is accomplished in plant cells in three steps, namely, reception (binding of the signal molecule to a specific receptor), transduction (release of the second messenger into the cytosol) and induction (alteration of cellular process). Being a free-radical, NO is involved in many physiological functions under adverse environmental conditions, especially salt-induced stress. However, to play a signaling role, a molecule should be structurally simple and highly diffusive and should be present in small amounts and should directly influence second messengers; NO possesses all of these properties (Hasanuzzaman et al. 2013c; Arasimowicz and Floryszak-Wieczorek 2007). Like other free radicals, the action of NO at the cellular level depends on the NO concentration in the cell. If the concentration increased markedly, nitro-oxidative stress is induced, but at a lower concentration, NO acts as a signal molecule (Arora

**Table 1** NO-induced regulation of ROS metabolism and antioxidant capacity in plants under salt-induced stress

| Plant species | Salinity treatment (dose and duration) | NO treatment (dose and duration) | Function of NO in ROS metabolism and antioxidant defense | References |
|---|---|---|---|---|
| *C. sativus* | 50 mM NaCl, 8 days | 100 µM SNP, 8 days | Decreased membrane permeability, MDA content, $H_2O_2$ content and $O_2^{\bullet -}$ generation<br>Increased activity of SOD, POD, CAT, and APX | Fan et al. (2007) |
| *C. arietinum* L. | 100 mM NaCl, 48 h | 0.2 mM SNP, 48 h | Decreased MDA content and relative injury<br>Increased APX and POX activity | Sheokand et al. (2008) |
| *Kosteletzkya virginica* | 200–400 mM NaCl, 5 days | 60 mM SNP, 5 days | Decreased MDA content<br>Enhanced activities of CAT, POD and SOD | Guo et al. (2009) |
| *T. aestivum* | 300 mM NaCl, 1–5 days | 0.1 mM SNP, 20 h | Decreased MDA content, $H_2O_2$ content and $O_2^{\cdot -}$ generation<br>Increased SOD and CAT activities | Zheng et al. (2009) |
| *C. arietinum* | 25 mM NaCl, 2, 4 and 6 days | 0.2 mM SNP, 2, 4 and 6 days | Decreased MDA and $H_2O_2$ content<br>Decreased relative membrane injury<br>Increased SOD and CAT activity | Sheokand et al. (2010) |
| *T. aestivum* | 300 mM NaCl, 72 h | 1 mM SNP, 24 h | Decreased MDA and $H_2O_2$ content<br>Enhanced AsA, GSH level<br>Increased MDHAR, DHAR, GR, GST, GPX, and CAT activities | Hasanuzzaman et al. (2011) |
| *L. esculentum* | 100 mM NaCl, 8 days | 100 mM SNP, 8 days | Decreased MDA content and $O_2^{\bullet -}$ generation<br>Enhanced activities of SOD, POD, CAT, and APX | Wu et al. (2011) |
| *Aegiceras corniculatum* | 300 mM NaCl, 30 days | 100 µM SNP, 30 days | Decreased MDA and $H_2O_2$ content<br>Increased GSH and polyphenol content<br>Enhanced GPX activity | Chen et al. (2014) |
| *Glycine max* | 80 mM NaCl, 16 days | 10 µM DETA, 16 days | Decreased $H_2O_2$ content<br>Increased APX activity | Egbichi et al. (2014) |
| *C. arietinum* | 100 mM NaCl, 45 days | 50 µM SNAP, 45 days | Decreased electrolyte leakage, $H_2O_2$ and MDA content<br>Increased the activities of SOD, CAT, APX and GR | Ahmad et al. (2016) |
| *T. aestivum* | 150 mM NaCl, 65 days | 0.1 mM SNP, seed pretreatment for 12 h | Decreased MDA and $H_2O_2$ content<br>Increased AsA and total phenol content<br>Enhanced activity of SOD, POD and CAT | Ali et al. (2017) |

**Table 1** (continued)

| Plant species | Salinity treatment (dose and duration) | NO treatment (dose and duration) | Function of NO in ROS metabolism and antioxidant defense | References |
|---|---|---|---|---|
| *Jatropha curcas* | 100 mM NaCl, 4 days | 75 µM SNP, seed pretreatment | Deceased TBARS and $H_2O_2$ content<br>Slightly increased AsA and GSH content<br>Increased activity of CAT and GR to some extent | Gadelha et al. (2017) |
| *B. juncea* | 100 mM NaCl, approximately 5 weeks | 100 µM SNP, 15 days | Both electrolytic leakage and MDA content decreased by 33%<br>Enhanced proline content by 42% | Gupta et al. (2017) |
| *P. sativum* | 100 mM NaCl, 7 days | 0.1 mM SNP, 7 days | Deceased MDA content by 22%<br>Increased activity of SOD, CAT, POX and APX | Yadu et al. (2017) |

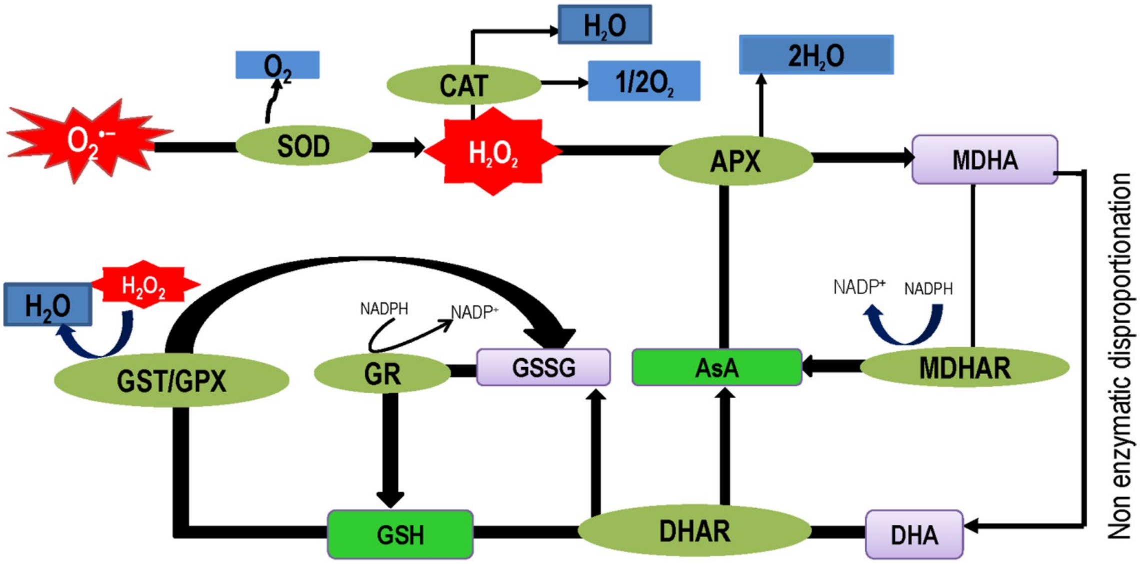


**Fig. 4** Key roles of nitric oxide (NO) under conditions of salinity for regulating various physiological mechanisms required for growth development and stress tolerance in plants

et al. 2016). NO is highly reactive due to the presence of an unpaired electron and can form a variety of intermediates (Hasanuzzaman et al. 2011). Under conditions of salt-induced stress, plant signaling cascades are activated, triggering specific defense mechanisms and the production of a signaling molecule that acts as a second messenger to defend against salinity (Hasanuzzaman et al. 2011; Fancy et al. 2017).

Nitric oxide can modulate a broad range of molecules, forming RNS and modifying protein activity, GSH biosynthesis, metal nitrosylation, tyrosine nitration/peroxynitrite formation, *S*-nitrosylation, *S*-glutathionylation, sulfhydration, etc., to sustain stress tolerance (Akter et al. 2015; Lamotte et al. 2015). Metal nitrosylation occurs when NO binds to transition metals in metalloproteins. The best example is the soluble guanylate cyclase enzyme, which undergoes such post-translational modifications (Arora et al. 2016). NO or the RNS target the cystine and tyrosine residues to modify the proteins by *S*-nitrosylation and nitration (Hasanuzzaman et al. 2013c). Nitration or tyrosine nitration are caused by the RNS peroxynitrite ($ONOO^-$), generated from NO and $O_2^{\bullet-}$. Previously, this nitration was thought to be harmful to plants, but studies have suggested that this nitration plays a signaling role. On the other hand, *S*-nitrosylation, the binding of NO to cysteine residues of target proteins, is the main process in signal transduction. Furthermore, *S*-nitrosylation can occur reversibly by transnitrosylation (Lamotte et al. 2015). Regardless of the mechanism of *S*-nitrosylation, these post-translational modifications (PTMs) have diverse roles in cellular processes and signaling cascades (Sevilla et al. 2015).

Nitric oxide signaling can be accomplished via inter- or intracellular interactions to generate the second messenger, such as, $Ca^{2+}$, cGMP, cADP-ribose, phosphatidic acid, and ROS (Besson-Bard et al. 2009; Leitner et al. 2009). After the initial discovery of cGMP in *Z. mays*, this molecule was proven to be an intermediate in the NO-signaling pathway in plant and animal systems, increasing $Ca^{2+}$ influx and reversible protein phosphorylation (Palavan-Unsal and Arisan 2009). Reports from different researchers have suggested that cGMP is a mediator of intracellular signaling, but to accomplishing this task, additional signals are necessary. For example, cGMP levels are increased by stress-induced ABA biosynthesis, which is essential for ABA-induced stomatal regulation (Hasanuzzaman et al. 2013c). Reports have also suggested that NO acts via cGMP and cADPR to alter $Ca^{2+}$ channels an increase the $Ca^{2+}$ content in the cytosol for various physiological functions under saline conditions (Arasimowicz and Floryszak-Wieczorek 2007). Increased cGMP levels can be lethal for plants and can cause cell destruction and PCD.

Both NO and NO-derived peroxynitrite combine with GSH to form GSNO with the involvement of the enzyme GSNO reductase (GSNOR), and the resulting GSNO further acts as a NO donor (Fancy et al. 2017). An important role played by GSNOR in plant cells under conditions of salt-induced stress is the limitation or alleviation of NO to combat stress (Hasanuzzaman et al. 2013c). Additionally, the stress is regulated by *S*-nitrosylation levels (Yu et al. 2014) and the absence of *S*-nitrosylation resulted in the accumulation of excess NO (Gong et al. 2014). Thus, GSNOR homeostasis is vital for stress tolerance (Corpas et al. 2013). The enzyme also catalyzed to formation of $NH_3$ and GSSG from GSNO, which was further reduced by GR to form GSH (Leterrier et al. 2012) and is critical for regulating the downstream effects of RNS and ROS in plants (Xu et al. 2015).

Abiotic stress has been reported to boost nitrosative bursts (Camejo et al. 2013; Ziogas et al. 2013), changing the *S*-nitrosoproteome, which is integral for stress signaling (Tanou et al. 2009). The reaction of NO with protein thiols—*S*-nitrosylation—is important in many biological systems during abiotic stress (Romero-Puertas et al. 2013). Exposure to salt-induced stress, for example, results in the *S*-nitrosylation of proteins and enzymes associated with different physiological processes, such as respiration, photorespiration, and antioxidant activity (Camejo et al. 2013). Slight changes in *S*-nitrosylation have been reported in cultured *Arabidopsis* cell suspensions upon exposure to salinity (Fares et al. 2011). Additionally, both short-term and long-term salt-induced stress decrease *S*-nitrosylation (Ziogas et al. 2013), but long-term salinity was found to reduce *S*-nitrosylation to a greater extent (Camejo et al. 2013). Furthermore, *S*-nitrosylation has a potential role in ABA-dependent stomatal regulation in response to conditions of stress (Roychoudhury et al. 2013). Thus, NO-signaling improved photosynthetic efficiency by improving stomatal conductance and RuBisCO activity (Fatma and Khan 2014). Via nitration, NO also produces metal proteins with sulfhydryl and nitro groups to afford resistance in opposition to stress (Leterrier et al. 2012).

Redox balance is very important to cope with salinity and is maintained by the AsA–GSH cycle, which is very important for detoxification of $H_2O_2$ and toxic MG in plants. Reports have suggested that NO-signaling helps to regulate this cycle via *S*-nitrosylation. Under salt-induced stress, the activities of four vital enzymes of the AsA–GSH cycle, namely, APX, DHAR, MDHAR, and GR, are hampered (Hasanuzzaman et al. 2011; Rahman et al. 2016). However, NO was reported to modulate APX via *S*-nitrosylation under salt-induced stress and to increase APX activity to efficiently detoxify $H_2O_2$, leading to a strong antioxidative defense against salinity. In contrast, salinity leads to *S*-nitrosylation of MDHAR, which limits the activity of this enzyme (Begara-Morales et al. 2014; Yang et al. 2015).

## Nitric oxide interacts with other signaling molecules to provide defense against salt-induced stress

Signaling networks in plants include a large number of receptors, messengers, transcription factors and enzymes that evolved to generating proper cellular responses (Memon and Durakovic 2014). Many biomolecules are involved in signal transduction in plants, such as plant hormones, ROS, RNS, MAPK, $H_2S$, polyamines, plant nutrients, lipids, and peptides, and almost all of these biomolecules interact with NO (Fig. 5). For example, during salt-induced stress, plants are subjected to ion toxicity along with physiological drought, which leads to stomatal closure. Guard cells that regulate stomatal opening and closure are very sensitive to salt-induced stress; in other words, salt-induced stress alters the signaling components (ROS, NO, $Ca^{2+}$) of guard cells. Therefore, interactions among these signaling molecules are vital for sustainable crop production.

Among signaling molecules, ROS and ROS intermediates are significant for signal transduction and participate actively during conditions of stress (Gill and Tuteja 2010). Among ROS, many researchers have suggested $H_2O_2$ to be a dynamic signaling molecule that participates in a variety

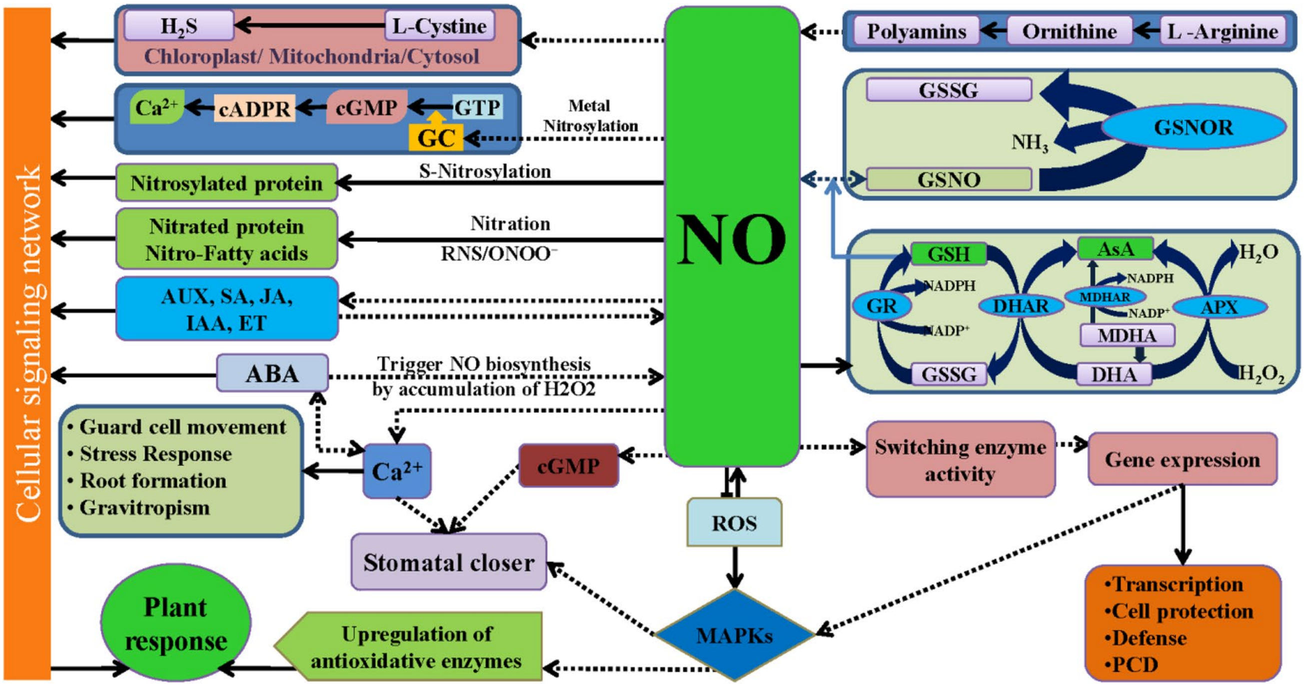


**Fig. 5** Interaction of nitric oxide (NO) with other signaling molecules in signal transduction pathways to provide a defense against salt-induced stress. *AsA* ascorbate, *APX* ascorbate peroxidase, *AUX* auxin, *cADPR* cyclic adenine dinucleotide phosphate ribose, *cGMP* cyclic guanosine monophosphate, *DHA* dehydroascorbate, *DHAR* dehydroascorbate reductase, *ET* ethylene, *ABA* abscisic acid, *GTP* guanosine triphosphate, *GC* guanylate cyclase, *RNS* reactive nitrogen species, *ROS* reactive oxygen species, *GR* glutathione reductase, *GSH* reduced glutathione, *GSSG* oxidized glutathione, *GSNO S*-nitrosoglutathione, *GSNOR S*-nitrosoglutathione reductase, *JA* jasmonates, *MDA* malondialdehyde, *MDHAR* monodehydroascorbate reductase, *MAPKs* mitogen-activated protein kinases, *NADPH* nicotinamide adenine dinucleotide phosphate (reduced), *PCD* programmed cell death, *SA* salicylic acid. Dotted lines represent activation/enhancement

of cellular responses and can induce several defense genes (Gill et al. 2016). In normal conditions, $H_2O_2$ can be generated in the cell from various sources. Experimental results have shown that there is a correlation between $H_2O_2$ generation and NO production (Delledonne et al. 2001). As NO is short-lived, it rapidly reacts with ROS to yield $NO_2$, which is degraded to nitrate (Bellin et al. 2013). In the cell, $H_2O_2$ formation may occur via $O_2^{\bullet-}$ (Tanou et al. 2009). It is likely that NO reacts with $O_2^{\bullet-}$ to form highly reactive peroxynitrite anions ($ONOO^-$), and subsequent cellular effects may then be induced by peroxynitrite (Bellin et al. 2013). However, under conditions of stress, $H_2O_2$ and NO can be generated simultaneously and can act together to accomplish many vital functions, such as cell death (Lin et al. 2012), senescence delay (Iakimova and Woltering 2015), root growth and development (Liao et al. 2011), and pollen-tube growth (Serrano et al. 2012). Moreover, these molecules interact closely with $Ca^{2+}$ and ABA to form a complex signaling network to tolerate salinity (Huang et al. 2015; Shi et al. 2015, Niu and Laio 2016). Under salt-induced stress, NO interacts with $Ca^{2+}$ and $H_2O_2$ to upregulating the $Na^+/H^+$ antiporter and reduce $K^+$ efflux (Lang et al. 2014). When plants face physiological drought during salt-induced stress, NO induces increased cytosolic $Ca^{2+}$ levels. This concentration gradient activates two channels (S-type and R-type) that release anions from the guard cell and cause depolarization. As a result, inward $K^+$ channels are deactivated and outward $K^+$ channels are activated. Therefore, there is a net loss in the $K^+$ ion gradient, which causes a loss in the turgor pressure, leading to closure of the guard cells (Garcia-Mata et al. 2003). Therefore, it is clear that NO acts in $Ca^{2+}$-mediated activation of cellular signaling (Palavan-Unsal and Arisan 2009; Gill et al. 2016).

Nitric oxide together with $H_2S$ upregulates several genes to increase $H^+$-ATPase activity in the plasma membrane and to maintain a high $K^+/Na^+$ ratio in salt-stressed seedlings (Shi et al. 2014; de Silva et al. 2017). In this process, the $Na^+/H^+$ antiporter enzyme is also activated, which compartmentalizes and removes cytosolic $Na^+$ (Chen et al. 2015). Hence, NO activates $H_2S$ to maintain redox homeostasis. In contrast, $H_2S$ hinders NO during stomatal regulation. Furthermore, NO induces reduction in total free PA, free putrescine (Put), spermidine (Spd), and polyamine oxidase (PAO) activity, as reported by Fan et al. (2007) in cucumber seedlings exposed to NaCl stress.

In plant systems, NO also activates MAPK signaling pathways (Baudouin 2011). Controversial reports have suggested that $H_2O_2$ or NO stimulate the activation of a MAPK, which can also be activated by salicylic acid (SA), jasmonic acid (JA) and ethylene (ETH) (Kumar and Klessig 2000; Hasanuzzaman et al. 2013c). Therefore, it remains unknown whether NO activates MAPK by itself or with the help of other messengers (Wrzaczek et al. 2010; Liu and He 2017). It has been reported that a NO-mediated cGMP-independent pathway is involved in activation of the MAPK signaling cascade induced by indole acetic acid (IAA) during the process of adventitious root formation in cucurbits (Pagnussat et al. 2004). Then, another study reported that $H_2O_2$ and NO activate MAPK leaf tissue with increased antioxidant activity (Zhang et al. 2007). Reports have also suggested that MAPK cascades act upstream or downstream of cell organelles such as chloroplasts, mitochondria, or peroxisomes to regulate ROS homeostasis or ROS signaling (Liu and He 2017). It has been suggested that several defense mechanisms against biotic and abiotic stress are triggered when NO and ROS are in equilibrium (Fancy et al. 2017). Furthermore, ROS and MAPK cascades interact with other signaling pathways to fine-tune the system response.

Studies have suggested that NO can form nitro-fatty acids ($NO_2$-FAs) via interactions with fatty acids. $NO_2$-FAs are produced by reactions of RNS with unsaturated fatty acids. These $NO_2$-FAs can participate in cellular signaling. Although scarcely studied, it has been suggested that $NO_2$-FAs are present in extra-virgin olive oil (EVOO). Mata-Pérez et al. (2017) reported the presence of endogenous nitrolinolenic acid ($NO_2$-Ln) in *A. thaliana* and showed the modulation of $NO_2$-Ln in the development of this plant in response to conditions of stress. Thus, the level of $NO_2$-Ln was found to be significantly high during stress, which proved that this molecule plays a role in signaling by directly releasing NO for further nitration or *S*-nitrosylation.

Nitric oxide is a major player in signaling networks, interacting with hormonal signaling pathways in plants. Reports have shown that NO interacts with auxins (AUX), gibberellins, ABA, ETH, jasmonic acid, brassinosteroids, and other plant hormones to regulate cellular metabolism as well as growth and development of plants. NO participates in the upstream and downstream regulation of plant hormones and modulates the biosynthesis, degradation, distribution of these hormones along with transportation and signaling (Hancock et al. 2011; Feng et al. 2013).

Nitric oxide, together with phytohormones, plays a vital role in improving the tolerance and acclimatization of plants in saline conditions. Plant hormones, such as ABA, ETH, and AUX, are transported from the roots to leaves of salt-stressed plants, thus triggering NO biosynthesis and/or distribution throughout the plant body (Molassiotis et al. 2010). It has been suggested that ABA stimulates $H_2O_2$ accumulation cells, which boosts NO biosynthesis, leading to MAPK activation and gene upregulation for the synthesis of antioxidant enzymes (Lu et al. 2009; Nawaz et al. 2017).

Another phytohormone, ETH, also acts as a signaling hormone and interacts with signaling cascades to enhance resistance during abiotic stress (Fatma et al. 2016b). Studies using *Arabidopsis* calli have reported that 100 mM NaCl triggered NO accumulation, resulting in increased ETH emission and plasma membrane $H^+$-ATPase activity to improve salt tolerance (Wang et al. 2010). Fatma et al. (2016b) also reported that S assimilation is promoted by NO, which is associated with ETH biosynthesis from the cystine-synthesis pathway. Therefore, it can be hypothesized that NO modulates ABA and ETH levels and regulates photosynthesis under conditions of salt-induced stress. Liu et al. (2015) reported that the growth of the root meristem in salt-stressed *Arabidopsis* was due to AUX and NO, whereas SA promoted NO generation in guard cells, leading to stomatal closure (Khokon et al. 2011). SA alleviated the toxicity of NaCl-induced salt stress by increasing proline accumulation. SA also interacts with NO-signaling cascades to modulate photosynthesis, decrease the accumulation of $H_2O_2$, improve $Ca^{2+}/Mg^{2+}$ uptake and reduced the uptake of $Na^{2+}$ under saline conditions (Dong et al. 2015). Kong et al. (2016) reported that NO upregulated CK biosynthesis and increased the longevity of leaves in cotton by reducing senescence.

## Nitric oxide-regulated gene expression during salt-induced stress

Studies with NO in plants have demonstrated the signaling functions of this molecule, which were seen to be correlated with plant developmental processes and stress defense mechanisms. Several studies have recently provided genetic evidence for the involvement of NO in gene induction and gene expression. Activation of the plasma membrane (PM) $H^+$-ATPase and the vacuolar $H^+$-ATPase enzymes and of the $Na^+/H^+$ antiporter by the action of the NO signal upregulated the $K^+/Na^+$ ratio (Zhao et al. 2004). Association of $H_2S$ and NO modulated the expression of $K^+/Na^+$ transporters in NaCl-affected roots of barley. $H_2S$ and NO amplified PM $H^+$-ATPase, the transcriptional levels of PM $H^+$-ATPase (*HvHA1*) and the $Na^+/H^+$ antiporter (*HvSOS1*), which decreased the cellular $Na^+$ levels. Interaction of $H_2S$ and NO augmented the transcriptional levels of the vacuolar $Na^+/H^+$ antiporter (*HvVNHX2*) and $H^+$-ATPase subunit β (*HvVHA-β*) and the protein expression of the vacuolar $Na^+/H^+$ antiporter (NHE1). Increased expression of these genes enhanced the vacuolar compartmentalization of $Na^+$, which decreased the cytoplasmic $Na^+$ levels (Chen et al. 2015). Foliar spraying with SNP increased the chlorophyll content, photosynthetic rate and expression of the LHCB gene in salt-affected cotton plants (after 22 days of stress). Expression of the *SOS1* and *NHX1* genes by SNP supplementation increased the $K^+$ levels and decreased the $Na^+$ levels in leaves. Decreased expression of ABA biosynthesis genes, *NCED2* and *NCED9*, led to downregulation of ABA content and delayed leaf senescence. Increased expression of cytokinin biosynthesis genes, IPT1 and ZR, and iPA content was induced by exogenous SNP supplementation (Kong et al. 2016). Enhanced expression of the *SOD, CAT* and *APX* genes were documented in *S*-nitroso-*N*-acetylpenicillamine (NO donor)-treated salt-affected chickpea plants, contributing to decreased electrolyte leakage and $H_2O_{2,}$ and MDA levels. Improved growth parameters, leaf relative water content, photosynthetic pigment production and osmolyte accumulation were demonstrated as being caused by NO treatment during salt-induced stress (Ahmad et al. 2016). Nitric oxide-mediated modulation of auxin and signaling decreased the root meristem size in salt-affected *Arabidopsis*. The mechanism of salt-induced root meristem growth inhibition was the repression of PIN expression (which was responsible for decreasing AUX levels) and stabilization of IAA17 (which suppressed AUX signaling) via increased NO levels (Liu et al. 2015). Published research reports regarding NO-mediated regulation of gene expression in plants under salt-induced stress are limited, and further research is required.

## Conclusions and future perspectives

The advancement of research focusing on NO in plants revealed various functions of NO. Nitric oxide rapidly reacts and interacts with other radicals/ROS, phytohormones and signaling molecules, including ABA, $H_2O_2$, NO, MAPK, and Ca, which not only modulate developmental processes, but also adaptive physiological responses under conditions of stress. The roles of PM $H^+$-ATPase and vacuolar $H^+$-ATPase and the effect of NO on these enzymes are vital for the regulation of the cellular $Na^+/K^+$ ratio and is one of the most important features in salt adaptation and tolerance of plants; we could not find much literature on this subject. The capacity to metabolize GSNO provides new perspective on the metabolism of NO in plants. Nitric oxide interacts with ROS and RNS, and the activity of GSNOR has been shown to regulate stress responses and PCD, but the mechanism is not defined. GSNOR plays a regulatory role in the post-translational modification of cysteine residues and thus may have roles in plant developmental processes and stress adaptation that are unknown to NO researchers. However, further in-depth studies are needed to elucidate the signaling behavior of NO in signal transduction in addition to transcriptional regulation and ion detoxification. The signaling function of NO is an indication of the effect of NO on gene expression. Several studies have recently provided genetic evidence for the involvement of NO in gene induction and gene expression, but resources and researchers are limited. The implementation of research plans to elucidate the unclear/unknown roles of NO and is necessary to understand the mechanism of NO-induced salt-stress tolerance in plants.

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