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Molecular Insights into the Role of Reactive Oxygen, Nitrogen and Sulphur Species in Conferring Salinity Stress Tolerance in Plants

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Abstract
Salinity stress is the major abiotic stress that affects crop production and productivity as it has a multifarious negative effect on the growth and development of the plant. Salinity stress stimulates the accumulation of reactive oxygen species (ROS) which is toxic to cells at higher concentrations. At lower concentrations, these molecules help in the mitigation of salinity stress through a series of signal transduction mechanisms. The respiratory burst by NADPH oxidase leads to an increase in ROS generation. It is a key signalling node in the plant gene network and helps to integrate the signal transduction with ROS signalling. Reactive nitrogen species (RNS) are free radical and non-radical reactive molecules that are also produced under salinity stress and lead to nitrosative stress by regulating SOS, *MAPK* dependent, Ca^{2+} dependent and G-protein dependent pathways. The reactive sulphur species (RSS) is a strong oxidizing agent that preferably attacks the thiol functional group. Activation of the different signalling components like ROS, RNS, RSS, SOS, Calcium, *MAPK* signalling and cross-talk between different signalling pathways and phytohormones have been considered as the main mechanism for ion homeostasis and Na^+ exclusion at the cellular level. These reactive species and their interaction upregulate the gene expression and phosphorylation level of different membrane transporters viz., PM H^+-ATPase and Na^+/ H^+ antiporter which might endure salinity tolerance in plants. This review aims to describe the interplay/crosstalk amongst reactive species and phytohormones under salinity stress. Moreover, mechanistic insight of reactive species-mediated stress regulation and the response has also been discussed which will be helpful for the development of stress-tolerant cultivars.

Keywords Salinity stress · Reactive oxygen species · Reactive nitrogen species · Reactive sulphur species · Phytohormone

Introduction

Salinity stress is one of the major abiotic stresses that drastically affects plant growth, development, crop production and productivity that further leads to the deterioration of the quality of the field and horticultural crops (Sanower and Sultan 2019; Lal et al. 2020; Chourasia et al. 2021). Soil salinity is identified as the main cause of land degradation thereby making the land inappropriate for the cultivation of crops (Basu et al. 2021). Generally, soil salinity is described by the presence of excess mineral ions viz., Na^+, Cl^-, SO_4^{-2} above the threshold level predominantly Na^+ ions in the soil (Chourasia et al. 2021). Salinity stress affects more than 1 billion hectares of land in about 100 countries around the world (Ivushkin et al. 2019). Salinity accounts for nearly 20% of the world's arable land and more than 50% of irrigated farmland (Basu et al. 2021). However, this number is expected to increase in the future which might be the

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consequence of unsuitable land management and artificial irrigation in the crop fields.

Salinity stress hinders the growth and development of plants by interfering with major physiological processes such as sodium ion toxicity, inducing early leaf senescence, nutritional disorders, membrane disorganization, necrosis and ultimately cell death (Kolomeichuk et al. 2020; Chourasia et al. 2021). Due to impaired root membrane selectivity, excessive Na^+ and Cl^- influx and K^+ efflux may cause ion imbalance that leads to K^+ deficiency because excess Na^+ ions compete with K^+ ions for the major binding site (Hussain et al. 2021). Salt stress induces the accumulation of reactive oxygen species (ROS) which includes $_1O^2$, O^{-2} and H_2O_2, which is detrimental to cells at higher concentrations as they trigger oxidative damage to nucleic acids, lipids and proteins (Devireddy et al. 2021). However, the ROS at lower concentrations might act as the signalling molecules which help in mitigating the salt stress by their signalling pathway. The RNS synthesized in the plant in the form of nitric oxide (NO) is responsible for conferring nitrosative stress in plants (Fatima et al. 2021; Tomar et al. 2021). Reactive sulphur species (RSS) has been proposed to denote a group of sulphur (S) related molecules (GSH) that plays an important role in preventing oxidative damage caused by salt stress (Astolfi and Zuchi 2013). The RSS itself is a strong oxidizing agent that preferably attacks the thiol functionality (Giles et al. 2002). So reactive oxygen, nitrogen and sulphur species (RONSS) plays a crucial role as signalling molecules in response to salt stress in plants (Antoniou et al. 2016). To cope with salinity stress, resulting from either osmotic stress or ionic toxicity, not only the RONSS but phytohormones have been reported to affect salt tolerance by regulating several physiological, biochemical and molecular mechanisms (Tiwari et al. 2020a, 2020b, 2021a; Kim et al. 2018; Wei et al. 2019). The crosstalk of these signalling molecules (ROS, RNS and RSS) with each other and phytohormones have been reported to be crucial in the adaptation of the plant under salinity stress.

The primary mechanism developed by the plant for salinity tolerance involves ionic homeostasis and regulation of the scavenging mechanism of toxic compounds in plant tissue. Plants use complex multi-component signalling pathways to rebuild cell homeostasis and promote survival in response to salt stress (Hussain et al. 2021). Activation of the different signalling components viz., like ROS, RNS, SOS, calcium, *MAPK* signalling and cross-talk between different phytohormones acts as a principal mechanism for ion homeostasis control and Na^+ exclusion at the cellular level. ABA is mainly induced in vascular tissues under salinity stress which is further exported from the biosynthesis site to the site where it is utilized (Martínez-Andújar et al. 2021). The uptake and distribution of ABA are stimulated to other cells by the specific ATP-dependent carriers thereby distribution and redistribution in the neighbouring tissues. The signalling mechanism of ROS molecules controls a wide array of biochemical processes, from the regulation of development and growth to responses to salinity stress (Suzuki et al. 2011). Besides, Ca^{2+} also plays an important role in the signalling of salt-mediated response which integrates many physiological and biochemical processes that regulate plant growth and development (reviewed by Manishankar et al. 2018). The salt overly sensitive (SOS) pathway which appears to be conserved in the almost all plant species have been studied in many plant species under salinity stress condition (Ji et al. 2013). MAPK signalling cascade is activated in stress conditions in plants including salinity stress (Xing et al. 2015). The genes involved in salinity stress tolerance can be divided into the following functional categories: (i) ion transport (*SOS*, *AtNHX* and H^+-ATPase genes) (ii) ROS scavenging (SOD, APX, CAT, GR) (iii) molecular chaperones (HSPs) and (iv) dehydration related transcription factors (Acosta-Motos et al. 2017; Kearl et al. 2019; Demirelbose et al. 2020).

A plethora of studies highlights the crucial role of ROS (Bose et al. 2014; Tanveer and Ahmed 2020), RNS (Saddhe et al. 2019), RSS (Nawaz et al. 2019) and phytohormone (Fahad et al. 2015) for salinity stress tolerance in the plants. However, to our knowledge, there are very limited reviews that have elucidated the cross-talk of all three reactive species with phytohormone. In this review, the interaction amongst reactive species (RONSS) along with their cross-talk with phytohormones has been discussed under salinity stress. *Per contra*, the mechanism of these three reactive species (RONSS) and their signalling component which acts upstream or downstream in salinity stress regulation and response have also been elucidated.

Phytohormones Interaction in Plants Under Salinity Stress

Phytohormones are important molecules for plants by which they regulate different stress responses (Zhang and Shi 2013). Previous reports revealed that the synthesis of endogenous plant hormones under osmotic/salinity stress conditions was correlated with tolerance (Fahad et al. 2015; Ryu and Cho 2015). During the plant life cycle from germination to maturity, auxin (IAA) modulates various growth and development processes of plants. These mechanisms rely heavily on the auxin concentration, gradient and spatiotemporal expression of receptors and signalling genes (Wiggins 2015). Under salt stress, there is a quick reduction in endogenous auxin availability due to strong regulation of auxin synthesis and these changes in endogenous levels provide convincing evidence about its role in response to these environmental changes (Sharma et al. 2015). Jung and Park

2011 found that under high salt levels in Arabidopsis auxin signals are incorporated into the NTM2 (membrane-bound transcription factor) which modulate seed germination via *IAA30* gene. Reports on expression micro RNA (miRNA) suggest that the salinity-mediated expression of miR393 negatively regulates *TIR1* and *AFB2* mRNA which is shown to have stabilization of Aux/IAA repressor, thereby leading to inhibition of auxin signalling (Iglesias et al. 2014). On the other hand, root architecture was also reported to be affected by auxin-mediated salinity stress (Pandey et al. 2019). Similarly, cytokinin was also reported to affect plant growth and developmental processes under abiotic stress (Reviewed by Ryu and Cho 2015; Pavlů et al. 2018). The positive and beneficial effect of exogenous application of kinetin under salinity stress might play a crucial role as a free radical scavenger and antioxidative mechanism involved in the protection of purine breakdown. Cytokinin might alleviate salinity stress by various mechanisms such as preservation of the photosynthetic mechanism, enhancement of antioxidant enzyme activity, improvement in water balance regulation, decreasing ABA concentration in wheat (Iqbal et al. 2006; Lal et al. 2021a), increasing proline content in brinjal (Wu et al. 2014) and modulation of plant growth and differentiation. Maggio et al. 2010 also reported in tomato plants that under salinity stress, exogenous application of gibberellic acid (GA) showed to have decreased stomatal resistance via enhancement of Cl^- ion in leaves. Ahmad et al. 2021 suggested that seed priming with exogenous GA application in pea under salinity stress might alleviate the expression of Na^+/H^+ antiporter (*NHX1* and *SOS1*) proteins that enhance Na^+ sequestration. Magome et al. (2008) reported that under salinity stress the endogenous GA level was reduced due to lowering of GA2-oxidase genes in *Arabidopsis thaliana*. However, the upregulation of the GA2-oxidase gene, expression of *DDF1* (*Dwarf and Delayed Flowering 1*) gene is responsible for salinity stress. Another classical hormone, ethylene has also emerged as one of the crucial mediator for salinity tolerance in plants such as *Arabidopsis thaliana* (Yang et al. 2013), rice (Yang et al. 2015), cucumber (Shakar et al. 2016) and tomato. In Arabidopsis, *EIN3* and *EIL1* regulate ethylene responses and confer salt tolerance but in rice Yang et al. 2015 observed that *MHZ6/OsEIL1*, a master transcription factor in the ethylene signalling pathway and analogous to *EIN 3* as well as *OsEIL2* (analogous to *EIL1*) negatively regulate salt tolerance. Yang et al. 2013 suggested that ethylene mediates salinity tolerance in *Arabidopsis thaliana* by retaining K^+ in shoots and roots rather than lowering tissue Na^+ content in plant tissues. Zhao et al. 2017 in their study on soybean found that exogenous ABA applications increased the expression of all *RAV* genes significantly under salinity stress. Out of all *RAV* genes in soybean, they characterized the *GmRAV-03* gene which might be involved in salinity tolerance. It was reported that RAV transcription factors play a role major in the regulation of the plant response to different abiotic stresses (Wang et al. 2020). The exogenous application of ABA in rice might upregulate the expression of OzCan1-1 (salt-stress-responsive calmodulin) gene which plays a crucial role in signalling and enhance proline accumulation (Sripinyowanich et al. 2013).

Salicylic acid also involved in the regulation of responses under different biotic and abiotic stresses. Recent studies revealed that SA plays a role in response to salinity stress also in many crops such as rice (Kim et al. 2018), strawberry (Samadi et al. 2019), cucumber (Miao et al. 2020), *Limonium bicolor* (Liu et al. 2019), safflower (Shaki et al. 2018) and barley (Pirasteh-Anosheh et al. 2017). Application of salicylic acid in all these crops under artificial salinity conditions different types of morphological and biochemical changes were observed which is mentioned in Table 1. Brassinosteroids are a group of naturally occurring plant steroidal hormones (Fahad et al. 2015) that are involved in different physiological, biochemical and molecular responses in plants. It is well known that they can also improve the detrimental effects of salinity on plant growth performance by external application in different crops like rice, *Arabidopsis* and cucumber. Application of brassinosteroid under salinity stress reported increased stomatal conductance, chlorophyll concentration, intercellular CO_2 concentration, net photosynthetic rate, antioxidant activity and osmolyte accumulation in plants (Fahad et al. 2015). Melatonin a low molecular weight compound having multiple functions protects the plants from various environmental conditions (Tiwari et al. 2021b; Lal et al., 2021b; Altaf et al., 2021). Elsayed et al. 2020 and Kamiab 2020 reported that exogenous melatonin application mitigates excess ROS production in peanut and pistachio seedlings under salinity stress.

Reactive Oxygen Species (ROS) Signalling Under Salinity Stress

Role of Reactive Oxygen Species (ROS)

The synthesis of ROS is an inevitable mechanism of aerobic life that is essential for the regulation of all biological processes in nature (Castro et al. 2021). Salt stress enhances the production and signalling of ROS in the cell which ultimately affects the phenotype of the plant. Under salinity stress, the stomatal conductance of the plant is affected, that reduces the supply of CO_2 in the plant, thereby increases the photorespiration rate in C_3 plants. The increased photorespiration rate is also responsible for the production of ROS (mainly H_2O_2). The hyperaccumulation of Na^+ and Cl^- ions occurs in the cytosol that affects the electron transport rate in the photosystem (PS) thereby inhibiting the electron acceptors in the vicinity of PS I and PS II (Baxter et al. 2014;

Table 1 Effect of different phytohormones under salinity stress

Crop	Exogenous application of phytohormone, dose and method of application	Salinity treatment and dose	Major effects	References
Wheat	Tryptophan, 4.89 mol L^{-1}	NaCl, 150 mM	Increased net CO_2 assimilation rate	Iqbal and Ashraf 2013
Maize	Auxin (IAA), 2 mM,	NaCl, 100 mM	Increased photosynthetic pigment concentration and leaf Na + /K + ratio, decreased Membrane permeability	Kaya et al. 2013
Ryegrass	6-benzylaminopurine, 25 µM, Foliar spray	NaCl, 250 mM	Increased activities of SOD, CAT, APX, MDAR, GR	Ma et al. 2016
Brinjal	6-benzyladenine, 10 µM, Nutrient solution	NaCl, 90 mM	Increased SOD, POX, ascorbate activity and decreased O_2^-, MAD, GSH	Wu et al. 2014
Wheat	Methyl Jasmonate, 0.1 µM	NaCl (2%)	Increased endogenous Cytokinin	Avalbaev et al. 2016
Sweet Sorghum	GA_3, 288 µM	NaCl, 50 mM	Promote seed germination and water absorption	Zhu et al. 2019
Common bean	Ascorbic acid, 1 mM GA_3, 0.05 mM	NaCl, 200 mM	Enhanced protein content, GPOX and decreased H_2O_2, MDA content	Saeidi-Sar et al. 2013
Barley	GA_3, 100 µM	NaCl, 100 mM	Increased shoot length and the dry shoot weight	Abdel-hamid 2016
Rice	GA_3, 10 µM, Seedling treatment	NaCl, 100 mM	Up-regulation of lipid biosynthesis	Liu et al. 2018
Pea	GA_3, 0.5 mM, Seed priming	NaCl, 100, 200, 300 mM	Inducing the antioxidant system, proline production, total phenol and flavonoid content, up-regulation of Na^+/H^+ antiporters	Ahmad et al. 2021
Okra	GA_3, 0.1 mM, Foliage spray Ascorbic acid (AsA), 0.1 mM, Foliage spray	NaCl, 100 mM	Increasing contents of chlorophyll, carotenoids, stimulating activities of antioxidant enzymes, Decreasing electrolyte leakage, H_2O_2 content and lipid peroxidation	Wang et al. 2019
Leaf lettuce	GA_3, 10^{-6} M, Nutrient solution	NaCl, 20 mM	Enhanced Biomass accumulation, leaf expansion, stomatal conductance, water and nitrogen use efficiency	Vetrano et al. 2020
Cucumber	Salicylic acid, 0.3 mM, Nutrient solution	NaCl, 50 mM	Increased RGR, leaf photosynthetic and RSA, Down-regulated expression of GL2 and RHD2 gene	Miao et al. 2020
Limonium bicolor	Salicylic acid, 0.08 mM, Nutrient solution	NaCl, 200 mM	Upregulation of gibberellic acid and alpha amylase activity, Low ABA content	Liu et al. 2019
Safflower	Salicylic acid, 1 mM, Nutrient solution	NaCl, 100 and 200 mM	Increased Glycine betaine, total soluble protein, carbohydrates, chlorophylls, carotenoids, flavonoid and anthocyanin contents	Shaki et al. 2018
Barley	Salicylic acid, 0.5, 1.0, 1.5 and 2.0 mM, Foliar application	NaCl (12 dS m^{-1})	Manipulation of ion distribution	Pirasteh-Anosheh et al. 2017
Soybean	Salicylic acid, 0.5 mM, Foliar application	NaCl, 100 mM	Increased proline, phenolics, soluble carbohydrates, phenylalanine ammonia lyase in roots and leaves and antioxidant enzyme (POX, CAT and polyphenol oxidase)	Ardebili et al. 2019

Table 1 (continued)

Crop	Exogenous application of phytohormone, dose and method of application	Salinity treatment and dose	Major effects	References
Strawberry	Salicylic acid, 100 µM, Foliar application	NaCl, 50 mM	Enhanced Root length, leaf weight, PS II activity, decreased MDA content	Samadi et al. 2019
Rice	Salicylic acid, 0.5 and 1 mM	NaCl, 100 mM	Decreased Na^+, lipid peroxidation, electrolyte leakage, CAT, SOD and APX	Kim et al. 2018
Rice	ABA, 100 µM, Spraying	NaCl, 0.5% (w/v)	Enhanced Proline, OsP5CS1 and OsP5CR gene expression	Sripinyowanich et al. 2013
Soybean	ABA, 200 µM	NaCl, 200 mM	Increased RAV genes expression	Zhao et al. 2017
Wheat	ABA, 10 µM	NaCl, 300 mM	Enhanced Proline content	Kaur and Asthir 2020
Cucumber	Melatonin, 1 µM	NaCl, 150 mM	Enhanced SOD, CAT, POD, GA activity and decreased ABA content	Zhang et al. 2014a
Cotton	ABA, 100 µM Mannitol, 200 mM	NaCl, 200 mM	Enhanced *GhMPK17* expression	Zhang et al. 2014b
Rice	Ethylene, 10 µL L^{-1}, Gaseous form using a syringe	NaCl, 200 mM	Knockdown of MHZ6/OsEIL1 and OsEIL2 in roots and coleoptiles	Yang et al. 2015
Arabidopsis	Ethephon, 30 µM	NaCl, 50, 100 mM	Retained K^+ in shoots	Yang et al. 2013
Cucumber	Calcium carbide, 30 mg, Powder form	NaCl, 150 mM	Increased the activities of amylase, SOD, CAT, soluble sugars, free amino acids and protein contents, Decreased H_2O_2 and MDA	Shakar et al. 2016
Brinjal	24-Epibrassinolide (EBR), 100 nM, Rooting media	NaCl, 90 mM	Increased chlorophyll con., net photosynthetic rate, stomatal conductance and intercellular CO_2 concentration, Decreased nonphotochemical quenching (NPQ)	Xue-Xia Wu 2012
Soybean	24-Epibrassinolide, 100 mM, Seed priming	NaCl, 100 mM	Increased antioxidant activity and osmolyte accumulation	Soliman et al. 2020
Rice	24-Epibrassinolide, 10^{-7} M, Seed priming	NaCl, 125 mM	Increased antioxidant activity, Decreased MDA content	Sharma et al. 2013
Grapevines	Melatonin, 50 µM	NaCl, 100 mM	Increased ethylene content	Xu et al. 2019
Rice	Melatonin, 20 µM	NaF (25 mg L^{-1})	Enhanced GA, ABA, Proline, CAT, GPOX, GPX activity and decreased IAA, MAD, Protein carbonylation, methylglyoxal, Fluoride bioaccumulation	Banerjee and Roychoudhury 2019
Cucumber	Melatonin, 100 µM	NaCl, 200 mM	Enhanced SOD, peroxidase, CAT, APX activity and ascorbic acid, glutathione content	Wang et al. 2016
Rice	Polyamine (Putrescine), 1 and 2 mM	NaCl, 200 mM	Enhanced GPX, GR activity	Ghosh et al. 2012

RSA Root system architecture, *RGR* Relative growth rate

Bose et al. 2014). Molecular oxygen receives these electrons and responsible for the reduction of O_2 or the formation of superoxide and other different reactive oxygen species (ROS) in plants (Shabala 2019; Chourasia et al. 2021). ROS are versatile reactive molecules that include both oxygen radicals (unpaired electrons) and other non-radicals mentioned in Table S1.

The major site for ROS synthesis is the subcellular compartment viz., chloroplasts (Suo et al. 2017), mitochondria (Che-Othman et al. 2017) and peroxisomes (Del Río and López-Huertas 2016) under abiotic stress conditions. In chloroplast, salinity stress can enhance ROS synthesis in the PSI and PSII are the crucial sites for production and signalling of ROS under illuminated conditions. Complex I and III of mitochondrial electron transport chain was reported as the major source for salinity stress-induced ROS production. The excess reduction of the ubiquinone pool under salinity stress might allow electrons to leak into molecular oxygen from complex I and III that results in the synthesis of superoxide ($O_2^{\cdot -}$) radical (Miller et al. 2010). The oxidative stress caused by higher salinity conditions might lead to the generation of the higher amount of H_2O_2 during photorespiration glycolate oxidase reaction, fatty acid β-oxidation and disproportionation of $O_2^{\cdot -}$ in the plant cell (Betti et al. 2016; Acosta-Motos et al. 2017). The cell wall-associated peroxidase that is located in the apoplastic region of the cell also generate O_2^- by oxidizing NADPH and transferring the electron to molecular oxygen (Qi et al. 2017).

The ROS molecules are produced in different metabolic pathways as a normal by-product (del Río 2015). The synthesis of ROS in the specific compartments are produced in a controlled manner, however, the synthesis of these molecules reported to be increased manifold under salinity stress condition. Thereby, uncontrolled salinity-mediated oxidative stress might lead to cellular damage and eventually cell death. Therefore, ROS production and ROS scavenging occur simultaneously in the cell thereby balancing production and the scavenging rate that maintains ROS level (Mittler et al. 2011). The response of ROS to salinity stress is expected to be different in the tissue and cell compartment. So to prevent damage under different salinity stress conditions, plants employ a mechanism that can maintain net photosynthesis with limited CO_2 supply, use alternative electron sinks or the antioxidant defences must keep active oxygen under control (Bose et al. 2014).

Mechanism of ROS-Mediated Response Under Salinity Stress

Salinity stress leads to oxidative burst in the cell which has a detrimental effect on the lipid membrane system (Naeem et al. 2020). The respiratory burst by NADPH oxidase (respiratory burst oxidase homologues, RBOHs) leads to an increase in ROS generation. It is a key signalling node in the plant gene network and helps to integrate the signal transduction with ROS signalling (Suzuki et al. 2011). Under salinity stress conditions, Ben Rejeb et al. 2015 reported higher activity of cell membrane-bound RBOSH in *Arabidopsis*. In contrast, Rodríguez et al. 2009 reported lower activity of cell membrane-bound RBOHS in maize plants. The intricate network of signalling in the plant against salinity is highly complicated that include metabolic and genetic changes. The plants also have evolved adaptive and survival strategies to counterbalance the changing environmental conditions such as salinity in which ROS play valuable roles as signal molecules. It includes systemic and retrograde signalling between chloroplast and nucleus in tobacco (Seo and Park 2021), programmed cell death in rice (Kim et al. 2014) and tobacco (Monetti et al. 2014) and maintenance of ionic balance and Na^+/K^+ content in rice (Shen et al. 2015).

The detrimental effects of ROS at higher concentrations in cells might lead to lipid peroxidation in cellular membranes (Su et al. 2019), DNA damage (Qiu et al. 2019), protein denaturation (Khan and Shahwar 2020), carbohydrate oxidation (Davaritouchaee et al. 2019), pigment breakdown (Nemat Alla and Hassan 2020) and impairment of enzymatic activity (Bharti and Barnawal 2019). The production of different types of ROS under salinity stress in maize (Mansour et al. 2005) revealed that ROS attack polyunsaturated fatty acids of membrane system (both cellular and organelle) lipids and induced peroxidation which formed small hydrocarbon molecules like malondialdehyde (MDA) and ketones (Gill and Tuteja 2010). Essential fatty acids such as linolenic and linoleic acid are more prone to the damage caused by hydroxyl and singlet oxygen radicals. Higher lipid peroxidation along with the increased MDA level was reported to be observed in rice (Khan and Panda 2008; Khare et al. 2015), *Cicer arietinum* (Kukreja et al. 2005), Glycyrrhiza (Pan et al. 2006) and maize (Carrasco-Ríos and Pinto 2014; AbdElgawad et al. 2016). The ROS molecule attacks protein molecules by the mechanism of covalent modification known as protein oxidation. Methionine and cysteine are more easily destroyed by singlet oxygen and hydroxyl radicals under abiotic stress conditions (Gill and Tuteja 2010). Under salinity stress conditions in canola susceptible genotypes (Sarigol), Bandehagh et al. 2011 observed a reduction in the abundance of Cu/Zn SOD, due to the production of high levels of hydroxyl radicals (OH·) in this genotype. The ROS molecules can remove the hydrogen atom in cysteine which results in the thiyl radical attached to other thiyl radicals forming disulphide bridges (Gill and Tuteja 2010).

Reports by Saha et al. 2015 in mungbean suggested that salinity stress can damage DNA due to the accumulation of ROS. Similarly, Zvanarou et al. 2020 also suggested the ROS-induced DSBs (double-strand breaks) and SSBs (single-strand breaks) in DNA under NaCl treated

Physcomitrella patens protonema. The mechanism behind the degradation of DNA might be due to the attack of ROS on purines, pyrimidines and the DNA backbone of DNA structure (Halliwell and Gutteridge 2015). Salt induced DNA damage has also been discovered in other plants, such as *Arabidopsis* (Roy et al. 2013) and mungbean (Ghosh et al. 2015). Therefore, the cell must need tight control of ROS content and its homeostasis in the cell to prevent the cell and nucleic acid from ROS-mediated oxidative damage. Different types of enzymatic and non-enzymatic antioxidants are responsible for the detoxification of ROS (Table S2 and S3).

Crosstalk of ROS with Phytohormone

Understanding ROS-hormonal crosstalk is essential to elucidate how plants control salinity-mediated redox metabolism under salinity stress (Mishra et al. 2017). ROS may interact with different signalling molecules or biosynthetic pathways of phytohormones (Fig. 1). ROS molecules are the effective regulators for hormonal interplay and associated developmental changes in the plant under salinity stress (Devireddy et al. 2021). Fu et al. 2019 in *Arabidopsis* characterized the crosstalk of ROS and IAA which enhanced the formation of primary root growth via *IAA-CONJUGATE-RESISTANT 4* (*IAR4*). They reported this cross-talk might regulate primary root growth under salinity stress through ROS-mediated auxin distribution. The distribution of auxin in different tissue-level might be beneficial to provide tolerance to plant stress conditions. Iglesias et al. 2010 reported in *Arabidopsis* that auxin signalling interacts with redox metabolism in case of adaptative response against oxidative stress and salinity. Similarly, Wang et al. 2015 in their study with *Arabidopsis thaliana* suggested that endogenous cytokinin overproduction resulting from inducible overexpression of *AtIPT8* negatively affects plant salt tolerance by regulating stress-sensitive gene expression, chlorophyll homeostasis and ROS production. Moreover, salinity stress tolerance is also reported to be conferred by GA content and signalling. GA biosynthetic pathway was suppressed (by down-regulation of the GA biosynthetic genes) by elevated ROS level which served as a stress signal that activated the multiple stimulus responses in cotton after 3 h of treatment with NaCl (Shi et al. 2015). Saline soil generates excess Na$^+$ ions and these ions stimulate ethylene-induced soil-salinity tolerance by its signalling mechanism. Ethylene might promote salinity tolerance by enhancing Na$^+$/K$^+$ homeostasis. In *Arabidopsis*, the ratio of Na$^+$:K$^+$ ratio is regulated by RBOHF-dependent as well as independent regulation of Na and K accumulation (Jiang et al. 2013). Peng et al. 2014 also found that ethylene pre-treatment might prevent the excess ROS accumulation in the cell which showed increased tolerance to salt stress in *Arabidopsis*. Whole-genome transcriptome analysis revealed Salt-Induced and EIN3/EIL1-Dependent (SIED) genes may contribute to salinity stress responses and amongst these genes, several genes encoding ROS scavengers were also involved. In *Arabidopsis*, the synthesis of ethylene was reported to improve salinity tolerance by modulating ROS redox, sucrose and antioxidant system (Yang et al. 2013; Tiwari et al., 2021c). Lin et al. 2012 suggested that in response to salinity stress ethylene insensitive

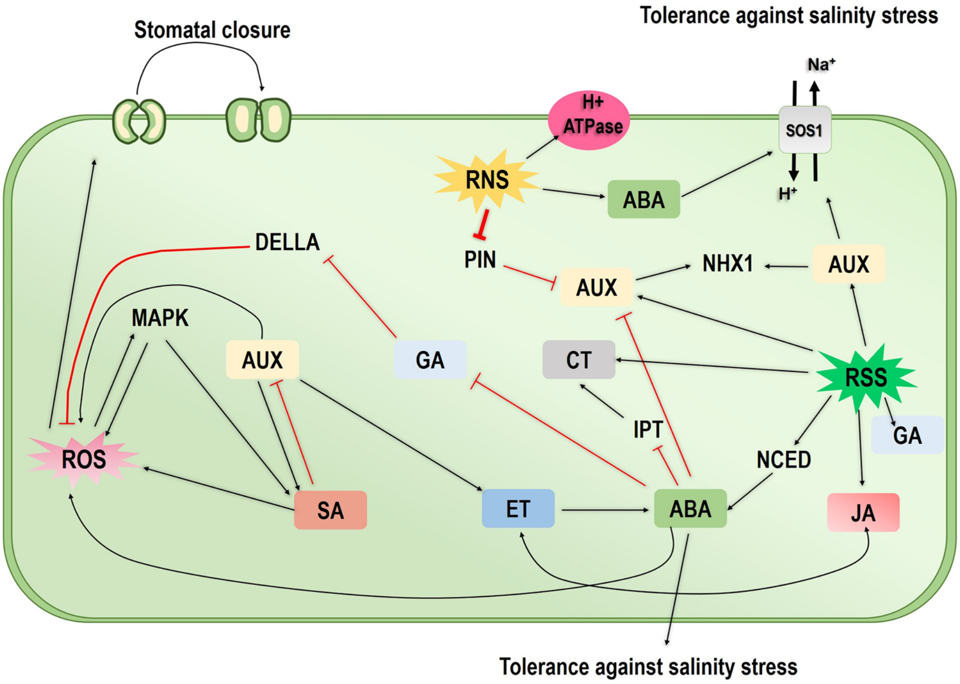

Fig. 1 A schematic model illustrating ROS, RSS, RNS–phytohormone crosstalk in relation to other hormone signals under salinity stress conditions. Blackline indicates activation, whereas the red line indicates the repression mechanism. *ABA* abscisic acid, *GA* gibberellins, *AUX* auxins, *MAPK* mitogen-activated protein kinase, *ROS* reactive oxygen species, *SA* salicylic acid, *ET* ethylene, *CT* cytokinin, *IPT* isopentyl transferase, *JA* Jasmonic acid, *NHX1* Na$^+$/H$^+$ exchanger 1, *RSS* reactive sulphur species (Color figure online)

and ethylene sensitive mutant of Arabidopsis showed promoted germination of seed which might be due to regulation of endogenous H_2O_2 concentration in germinated seeds. *AtrbohD* and *AtrbohF* are two genes expressing NADPH oxidase enzyme which involved in the impairment of ABA signalling under salinity stress (Kwak et al. 2003). *AtrbohD* and *AtrbohF* gene-mediated synthesis of ROS regulate Na^+/K^+ homeostasis in the cell which might help ABA-mediated stomatal regulation, increased ABA-induced cytosolic Ca^{2+} and ABA-mediated activation of plasma membrane Ca^{2+}-permeable channels in guard cells (Ma et al. 2012). Luo et al. 2021 suggested that an elevated level of *RbohD* gene which is responsible for more ROS accumulation is dependent on *ABI4* (Abscisic Acid-Insensitive 4). *ABI4-RbohD/VTC2* (Vitamin C Defective 2) regulatory module integrates both cell membrane integrity and ROS metabolism, ultimately repressing seed germination under salinity stress. Rady 2011 in their study with bean observed that 24-Epibrassinolide showed enhanced level of the antioxidant systems (SOD, CAT, POX, GR and proline) under salinity stress.

Reports also suggested that novel phytohormones such as strigolactones (SL) are also involved in the regulation of stress adaptation (Ha et al. 2014). In Arabidopsis under salinity stress, it was reported that *SsMAX2* (a key component in SL signalling) plays a pivotal role in the regulation of salinity-mediated oxidative stress via the regulation of antioxidative enzymes. Liu et al. 2020 in their study with rice root tip under salt stress observed increased expression of DEGs which encodes respiratory burst NADPH oxidases (*OsRBOHA* and *OsRBOHF*), calcium-dependent protein kinase (*OsCDPK*) and calcineurin B-like/calcineurin B-like-interacting protein kinase (*OsCBL/OsCIPK*). The role of different phytohormones and their effects on plants under salinity stress condition has been mentioned in Table 1. Further, researches on these versatile signalling switches are required which will provide the future path for the plant to adapt under dynamic environment.

Reactive Nitrogen Species (RNS)-Mediated Response to Salinity Stress

Role of Reactive Nitrogen Species (RNS)

Similar to ROS, reactive nitrogen species (RNS) are another set of free radical and non-radical reactive molecules that are synthesized under salinity stress, thereby leading to nitrosative stress (analogous to oxidative stress) (Tan et al. 2007; Kapoor et al. 2019). The RNS is synthesized from nitric oxide ($^{\cdot}$NO) which plays a vital role in plant growth, development, physiological processes and key signalling mechanism in different processes that are involved in various stress tolerance mechanisms (Molassiotis et al. 2010; Mur et al. 2013). The RNS synthesis is initiated in the plant with a quick reaction of nitric oxide ($^{\cdot}$NO) with superoxide ($O_2^{\bullet-}$) to form peroxynitrite (ONOO–) which is a powerful oxidative agent. Peroxynitrite molecules further react with new molecules to form other different types of RNS (Ferrer-Sueta et al. 2018). The RNS molecules that are produced in the plant in response to abiotic stress are$^{\cdot}$NO, nitrogen dioxide ($^{\cdot}NO_2$), S-nitrosoglutathione (GSNO), nitrate (NO_3^+), non-radicals S-nitrosothiols, peroxynitrite ($ONOO^-$), dinitrogen tetroxide (N_2O_4), nitrosonium cation (NO^+), dinitrogen trioxide (N_2O_3), nitroxyl anion (NO –), nitryl chloride (NO_2Cl) and nitrous acid (HNO_2) (Laxa et al. 2019; Kapoor et al. 2019).

RNS and its derivatives are generated in the apoplastic regions (Farvardin et al. 2020), cytoplasm, plasma membrane and different subcellular organelles such as the chloroplast, mitochondria (Gupta et al. 2018) and peroxisomes (Corpas et al. 2020) during salinity stress. Despite intensive work revealing its diverse functions, reactivity, signalling molecule and nitrosative stress, NO production pathway in plants is still poorly understood and remains one of the most puzzling topics in the field (Astier et al. 2018). NO can originate from different paths in the cell, however, two modes of RNS production viz., oxidative pathway (using nitric oxide synthases (NOSs) enzyme) and the reductive pathway (reduction of nitrites to NO using nitrate reductase (NR) enzyme) were mainly proposed. In Arabidopsis, Zhao et al. 2007 used NOS inhibitor (L-NNA) and observed a very low endogenous level of NO under salinity stress, which favoured the oxidative pathway of NO production. A reductive pathway under salinity environments was observed by Kataria et al. 2020 in soybean by using nitrate reductase inhibitor (sodium tungstate), resulting in low NO endogenous level.

The RNS synthesized in the plant in the form of NO is responsible for conferring nitrosative stress in plants. RNS signalling can mitigate the adverse effects of high salinity by regulating SOS pathway in rapeseed (Zhao et al. 2018), MAPK dependent pathway in maize (Bai et al. 2011), Ca^{+2} dependent pathway in the roots of *Hylotelephium erythrostictum* (Chen et al. 2019) and G-protein dependent pathway in Arabidopsis (Li et al. 2009). Recent reports on the role of RNS revealed positive effects in response to salinity stress in different plant species such as rice (Cai et al. 2015), maize (Kaya and Ashraf 2020), wheat (Sehar et al. 2019), tomato (Manai et al. 2014), citrus (Tanou et al. 2012), cucumber (Campos et al. 2019) and halophytes (Chen et al. 2013). Several studies demonstrate the beneficial role of the application of exogenous NO under salinity stress in the plant has been highlighted in Table 2.

Table 2 Effect of exogenous application of NO donor compounds to plants subjected to different salinity treatment

Crop	NO donor compounds, dose and method of application	Salinity treatment and dose	Function of NO in plants/physiological effects	References
Broccoli	Nitric oxide, 0.02 mM, Seed treatment and foliar spray	NaCl, 120 mM	Reduced MDA, H_2O_2 content and Enhanced SOD, POD and CAT activity	Akram et al. 2020
Pepper	SNP, 150 µM, Foliar spray	NaCl, 150 mM	Decreased MDA and H_2O_2 content	Shams et al. 2019
Strawberry	SNP (0.1 mM) or sodium ferrocyanide (0.1 mM), Foliar spray	NaCl, 50 mM	Reduced electrolyte leakage, MDA, H_2O_2 content, reduced SOD and CAT activity and increased POD activity	Kaya et al. 2019
Tomato	GSNO, 400 µM, Root treatment	NaCl, 100 mM	Induced H_2S biosynthesis for mitigation of oxidative stress	da-Silva et al. 2018
Rice	SNP, 0.25 mmol/L	NaCl, 150 mmol/L	High biomass production and increased the expression levels of OsHIPP38, OsGR1 and OsP5CS2 gene	Adamu et al. 2018
Maize	2,2′-(hydroxynitrosohydrazono) bis-ethanimine (DETA/NO), 10 µM, Nutrient solution	NaCl, 150 mM	Increased the activity of SOD	Klein et al. 2018
Wheat	SNP, 0.1 mM, Seed priming	NaCl, 150 mM	Enhanced SOD, POD and CAT activity, Decreased MDA and H_2O_2 content, Increased AsA, Pro and total phenolic content	Ali et al. 2017
B. junceaa	SNP, 100 µM, Foliar Spray	NaCl, 100 mM	Electrolytic leakage and MDA content decreased, Enhanced proline content	Gupta et al. 2017
Pea	SNP, 0.1 mM	NaCl, 100 mM	Deceased MDA content, Increased SOD, CAT, POX and APX activity	Yadu et al. 2017
Jatropha	SNP, 75 µM, Seedling priming	NaCl, 100 mM	Increased, GSH, AsA contents as well as CAT and GR enzyme activities	Gadelha et al. 2017
Cotton	SNP, 300 µM, Foliar Spray	NaCl, 150 mM	Decreased Na^+ and ABA contents and increased K^+ and cytokinin	Kong et al. 2016
Maize	SNP, 3 and 6 mg L^{-1}, Foliar Spray	NaCl, 100 mM	Reduced Na+, MDA, H_2O_2 level but increased N, K^+, Ca^{+2} and P	Kaya et al. 2015
Tomato	SNP, 100 and 300 µM	NaCl, 120 mM	Increased SOD, APX, GR, peroxidase, NR and NiR activities	Manai et al. 2014
Kandelia obovata	SNP, 100 µM, Nutrient solution	NaCl, 400 mM	Increased the protein expression of plasma membrane H^+-ATPase and vacuolar Na^+/H^+ antiporter	Chen et al. 2013

Mechanism of RNS on Plant Cell

Salinity stress conditions in the soil might trigger NO metabolism in plants. NO metabolism leads to an increase in NO synthesis in rapeseed which showed an increase in the amount of S-nitrosylation (Zhao et al. 2018) and nitration in sunflower proteins (David et al. 2015) under salt stress. Several studies report that NO appears to modulate and reduce electrolyte leakage in strawberry (Kaya et al. 2019), lower synthesis of MDA and H_2O_2 content in wheat (Ali et al. 2017), induced H_2S biosynthesis for mitigation of oxidative stress in tomato (da-Silva et al. 2018) and increased the protein expression of plasma membrane H^+-ATPase and vacuolar Na^+/H^+ antiporter in *Kandelia obovata* (Chen et al. 2013) under salinity stress. Nitric oxide and NO-derived molecules can alter target proteins by the phenomenon of post-translational modifications (PTMs) which plays a pivotal role in the modification of RNS signalling pathways (Chaki et al. 2020).

RNS modify protein residues and modulate a broad range of molecules like tyrosine nitration, sulphydration, metal nitrosylation, S-glutathionylation and S-nitrosylation in response to a stressful environment (Hasanuzzaman et al. 2018b). The binding of different RNS like NO to cysteine and peroxynitrite ($ONOO^-$) to a tyrosine of target proteins caused S-nitrosylation (Zhang and Liao 2019) and tyrosine nitration (NO_2-Tyr), respectively, and this phenomenon can alter the function of different proteins. Similarly, enhanced level of total S-nitrosylation following salt stress has also been reported in citrus (Tanou et al. 2012), *Arabidopsis* (Fares et al. 2011), pea (Camejo et al. 2013; Begara-Morales et al. 2015), rapeseed (Zhao et al. 2018) and sunflower seedlings (Jain et al. 2018). This tyrosine nitration may be a good biomarker or footprint for nitrosative stress in many crop plants (Arora and Bhatla 2017). Most studies focus on the tyrosine nitration in plants. However, in the protein constitute of amino acid such as cysteine, tyrosine, methionine and tryptophan are preferentially nitrated. Tyrosine nitration as a nitrosative stress has been reported in *Arabidopsis* (Corpas et al. 2009), sunflower (David et al. 2015) and citrus (Tanou et al. 2012). It is very important to understand here that this PTM's is not always harmful to plants because in some cases this nitrosylation of cysteine residues inhibit the carbonylation phenomenon in plants so ultimately prevent oxidative damage to proteins (Tanou et al. 2012). Therefore, it is cleared that the above PTMs are an integral part of the salt stress signalling intermediates that are controlled by different RNS molecules. Exogenous NO is also beneficial for plants subjected to salinity, where it increases salinity tolerance via different mechanism mentioned in Table 3. Therefore, NO-mediated mechanisms have been identified in plants under salinity stress, most of which can improve plant growth and reproduction (Sharma et al. 2020).

RNS Crosstalk with Phytohormone

Previous reports suggested that NO interplays with signalling pathways of different phytohormones (Fig. 1) to control metabolism, growth and development in plants under different physiological conditions (Sanz et al. 2015; Nawaz et al. 2017; Asgher et al. 2017; Zhou et al. 2021). Several synergistic and antagonistic interactions have also been observed during NO and phytohormone crosstalk.

The elevated NO accumulation in *Arabidopsis* under to salt stress down-regulates the expression of *PIN* (*PIN-FORMED*) genes, leading to the reduction of auxin levels and stabilizes *IAA17* (*INDOLE-3-ACETIC ACID17*)/*AXR3* (*AUXIN RESISTANT3*), thereby repressing auxin signalling (Liu et al. 2015). Under salinity stress condition in cotton, Kong et al. 2016 observed that NO plays an important role in delaying leaf senescence thereby maintaining plant growth. The NO-mediated delay of senescence might be due to increased expression of NHX1, SOS1 genes, cytokinin biosynthesis genes, K^+ content and decreased the ABA biosynthesis genes (NCED2, NCED9) and Na^+ content in leaves. Poór and Tari 2011 also found an antagonistic relationship between NO and ethylene in tomato cell suspension cultures treated with NaCl (100 and 250 mM). However, ethylene and NO act synergistically in stimulating plasma membrane H^+-ATPase activity to regulate ionic homeostasis under salinity stress in *Arabidopsis*. Therefore ethylene might be a part of the downstream signal mechanism in NO-mediated regulation of salinity stress (Wang et al. 2009). Santos et al. 2020 studied ABA-NO-Auxin integrated signalling network in tomato roots in response to salinity stress condition and noted that NO promotes auxin distribution as well as modulates plasma membrane H^+-ATPase activity and NO is required for ABA-mediated root antioxidant enzyme induction. Reports on cucumber seedlings under salinity stress revealed that NO might enhance salinity tolerance by regulation of free polyamines (putrescine, spermidine and spermine) proportion (Fan et al. 2013). Arora and Bhatla (2017)

Table 3 Role of sulphur under salinity stress

Crop	Salinity treatment and dose	Sulphur donor and dose	Effects	References
Capsicum	NaCl, 100 mmol L^{-1}	GSH (1 mmol L^{-1}) + Sodium hydrosulphide (0.2 mmol L^{-1})	Accelerating Ascorbate–Glutathione Cycle and Glyoxalase System	Kaya et al. 2020
Lettuce	NaCl, 40 mM	S, 1.5 g L^{-1}	Reduction in H_2O_2 level, SOD and APX activity increased, lower Na^+/K^+ ratio	Freitas et al. 2019
Tomato	NaCl, 100 mM	GSH, 50 mM	SOD, POD and CAT activity increased	Zhou et al. 2017a, b
Mungbean	NaCl, 200 mM	GSH, 1 mM	Higher activities of APX, MDHAR, DHAR, GR, SOD, CAT and GPX	Nahar et al. 2015
Barley	NaCl, 100 mM	Sulphate, 1.2 mM	Enhanced GSH biosynthesis so reduced ROS	Astolfi and Zuchi 2013
Mustard	NaCl, 100 mM	S (200 mg S kg^{-1} soil), GSH (1 mM)	Increased activity of CAT, APX and GR, increased GSH content	Fatma et al. 2014
Mustard	NaCl, 100 mM	Sulphate, 2 mM	Reduced the content of H_2O_2 and lipid peroxidation, Increased GSH biosynthesis	Nazar et al. 2014

studied the interaction of melatonin and NO under salinity stress in sunflower seedlings and observed differential modulation of SOD isoforms (Cu/Zn SOD and Mn-SOD). Stress tolerance response might occur due to transportation of metabolic signals that leads to melatonin-mediated mitigation of nitrosative and oxidative stress (Sun et al. 2021). Ahanger et al. 2020 in their study with salt-stressed *Vigna angularis* noticed that combined application of salicylic acid and NO proved much more beneficial in mitigating salt stress as compared to their individual application. This was correlated with the upregulation of the antioxidant system to counter the deleterious effect of salinity stress. Similar types of results were obtained by Ahmad et al. 2018 in *Solanum lycoperscum* for mitigating NaCl stress by supplementation of jasmonic acid and nitric oxide. The reports on the cross-talk of phytohormone and RNS under salinity stress are elusive which need more in-depth research on these aspects.

Reactive Sulphur Species (RSS)-Mediated Response to Salinity Stress

Role of Reactive Sulphur Species (RSS)

Reactive sulphur species (RSS) is a molecule that contains sulphur compounds (GSH and thiol group) that have strongly nucleophilic properties and are suitable for biological redox reactions which play a vital role in preventing oxidative damage caused by salinity stress (Nazar et al. 2011). The enzymes of the sulphur assimilation pathway are induced by the application of sulphur under salinity stress that helps to neutralize or eliminate ROS in mustard and other plant species (Fatma et al. 2013; Nazar 2014; Nazara et al. 2015). In these molecules, sulphur is present in non-oxidizing states but some naturally occurring molecules like sulphinic and sulphonic acids where sulphur is present in higher oxidation states (Giles et al. 2001) that gives an idea of the involvement of reactive sulphur species (RSS)-mediated signalling. The term RSS has been proposed for the first time in animal systems where sulphur related molecules are formed under in vivo oxidative stress. These molecules include thiyl radicals ($RS^{\cdot}$), disulphide (RSSR) disulphide-S-monoxides [RS(O)SR] disulphide-S-dioxides [$RS(O)_2SR$] and sulphenic acids (RSOH) (Giles et al. 2001; Jacob et al. 2004).

Till now, amongst all the reactive species ROS and RNS have gained significant attention and works of literature are available on this aspect but the involvement of RSS is also an important area to understand salinity stress signalling conditions in the plant. Moreover, these molecules also mitigate the abiotic stress condition through the regulation of sulphur metabolism as well as the synthesis of various sulphur metabolites (Ijaz et al. 2019). Sulphur attenuated the toxic effects of salinity by better uptake of P and K and a lower Na^+/K^+ ratio in lettuce plants (Freitas et al. 2019). S-mediated alleviation of salinity stress was reported to be achieved in mustard through higher GSH synthesis and lower concentration of Na^+ and Cl^- ions (Fatma et al. 2014). Moreover, Salicylic acid application also alleviates the salt-induced decrease in photosynthesis mainly through inducing the activity of ATP-sulphurylase (ATPS) and nitrate reductase (NR) enzyme in mungbean (Nazar et al. 2011).

Mechanism of RSS on Plant Cell

The RSS itself has strong oxidizing agents that preferably attack the thiol functionality (Giles et al. 2002). They regulate and modulate the redox status of biological thiols and disulphides, thereby positively act towards conferring stress tolerance (Corpas and Barroso 2015; Nawaz et al. 2019). Recent reports on the pepper plant suggested that GSH-induced salinity stress tolerance can be achieved by increasing H_2S due to the activation of the L-DES enzyme (primary producer of H_2S) (Kaya et al. 2020) and therefore H_2S may improve the activities of antioxidant enzymes under saline stress. Sulphur and its reactive compounds are actively involved in different biochemical reactions due to its wide range of oxidation states. Like nitric oxide and superoxide, thiols are key molecules with formal oxidation states of S-2 that are an important resource for RSS production. The synthesis of novel compounds and molecules in plant peroxisomes such as GSH, GR, GSNO and sulphite oxidase (SO) shows the participation of these species in the metabolism of sulphur (Ijaz et al. 2019). Different types of RSS and their major function are mentioned in Table 3.

There is also some research evidence that validates the signalling mechanism of reactive sulphur species such as GSH, H_2S, methionine (Met), cysteine (Cys), phytochelatin (PC), ATP-sulphurylase (ATPS) and protein thiols**.** Capaldi et al. 2015 reviewed the crucial mechanisms involved in S containing compound-mediated oxidative stress in plants. In presence of S, the GSH content in barley and mustard (Astolfi et al. 2010; Nazar et al. 2014), the ratio of GSH/GSSG in D*actylis glomerata* (Zagorchev et al. 2012), AsA content in capsicum (Kaya et al. 2020), the ratio of AsA/DHA in mungbean (Nahar et al. 2015), APX in mungbean and lettuce (Nahar et al. 2015; Freitas et al. 2019), GR in mustard (Fatma et al. 2014) and CAT in tomato (Zhou et al. 2017a, b) were reported to be improved in different crops under salinity stress condition. Exogenous application of S in the plant might mitigate the deleterious effect of salinity by lowering Na^+/K^+ ratio, enhanced P and K uptake and enhancing activities of antioxidant enzymes (CAT and APX) (Freitas et al. 2019). Similarly, exogenous application of GSH also showed to have increase tolerance against salinity-mediated oxidative stress by increased antioxidant enzyme system, regulation of GSH biosynthesis and maintenance of cellular redox homeostasis (Zhou et al. 2017a, b).

In salt-treated plants of barley Astolfi and Zuchi 2013 observed that sufficient application of sulphur allows adequate GSH synthesis (high-thiol concentration) thereby preventing the adverse effects of ROS on photosynthetic machinery. Moreover, external application of GSH and S to the mustard plant was reported to have increased endogenous GSH production with improved photosynthetic rate and growth parameters (Fatma et al. 2014). In the aforementioned study, Fatma et al. 2016 suggested that the combination of the application of NO (sodium nitroprusside) and sulphur showed increased activity of ATP-sulphurylase (ATPS), CAT, APX and GR. Therefore, S and NO-mediated increase in activities of antioxidant enzymes might improve the photosynthetic performance of the plant. S-methyl methionine was also reported to be involved in the salinity tolerance of *Arabidopsis thaliana* plants during germination and early growth stages (Ogawa and Mitsuya 2012). Zagorchev et al. 2012 also showed that total glutathione (GSH + GSSG) concentrations and upregulation of Cys synthesis are crucial for scavenging ROS under salinity stress. Overall, sulphur or sulphur-containing compounds are integral molecules in the alleviation of salinity stress in plants (Nazar et al. 2011; Khan et al. 2013). Moreover, glutathione molecules might act as a centre of 'hub' molecule in the cellular metabolism and redox signalling mechanism under salinity stress.

Crosstalk of RSS with Phytohormone

Sulphur can interact with different phytohormones (Fatma et al. 2013; Hasanuzzaman et al. 2018a) such as AUX, GA, CK, ABA, ET, JA and SA under salinity stress conditions and thereby positively regulates plant defence by accumulating GSH (Fig. 1). Therefore, the need for phytohormones is essential to cope with salinity stress through antioxidant enzymes and for S-regulation. Koprivova et al. 2008 studied a complex signalling network in Arabidopsis roots under salinity stress and found that GA signalling is essential for the increase in APR (adenosine 5′-phosphosulphate reductase: a key enzyme of sulphate assimilation) mRNA level under salt treatment. The improvement of photosynthesis might be controlled by S-induced alleviation under salinity stress conditions (Nazar et al. 2014). Recent reports suggested that the mustard plant when treated with 100 mM NaCl stress along with the ethephon showed an increased level of the antioxidant system, ABA accumulation in guard cells, enhanced photosynthetic efficiency and maintenance of membrane stability (Fatma et al. 2021). Cao et al. 2014 found that synthesis of the phytohormone ABA in developing seedlings and germinating seeds of *Arabidopsis*, was dependent on sufficient Cys availability and as a consequence affected by external sulphate supply. The increase in leaf sulphur (S) content through the higher activity of serine acetyltransferase (SAT) and ATP-sulphurylase (ATPS) by external salicylic acid application was associated with the higher accumulation of glutathione (GSH) and lower levels of oxidative stress (Nazara et al. 2015). The application of salicylic acid showed an increased photosynthetic rate which might be due to the increased activity of nitrate reductase and antioxidant mechanism (Nazar et al. 2011).

Tripartite Interaction Mechanism of RONSS Under Salinity Stress

One reactive species affects the production, perception and further signalling of another reactive species. RNS and ROS produce peroxynitrite (ONOO −) which generates new signals when they react with H_2S (Fig. 2). The ROS synthesis regulates the level of RNS (mainly NO) in the cell which regulates the signalling mechanism. The salinity-mediated synthesis of H_2O_2 by NADPH oxidase enhanced the production of NO which prevent the further accumulation of excess ROS in the cell. The ROS synthesis under salinity stress also enhances the production of RSS (H_2S or GSH). NO react with GSH to form GSNO which is further reduced by GSNO reductase into oxidized glutathione (GSSG). Higher NO accumulation in the cell leads to inhibition of GSNOR and thereby preventing GSNO degradation in the cell.

Gohari et al. 2020 demonstrated a positive interplay between H_2O_2 and NO to counter salinity stress in basil (*Ocimum basilicum* L.) plant and reported enhanced guaiacol peroxidase (GP) and APX activity after combined treatment of H_2O_2 and SNP (NO donor). Hajihashemi et al. (2020) studied crosstalk between H_2O_2, NO and Ca^{2+} under the saline condition in quinoa and recorded enhanced amylase activity and a strong positive correlation between germination rate with germination index and relative seed germination which ultimately mitigated the adverse effect of salinity. Dinler et al. (2014) studied the interplay between nitric oxide (NO) and Glutathione-s-transferases (GSTs) in soybean plants in response to salinity stress and suggested that NO regulates the expression of GST genes and isoenzyme activities (GST1 and GST4) were significantly induced after SNP pretreatment. Tanou et al. (2012) in their study with citrus plants under salinity conditions demonstrated that pre-exposure to NO and H_2O_2 alleviated the negative effect of salinity and their interaction with each other either systematically or locally in citrus plants. In the same study, they noticed that on one side H_2O_2 pretreatment stimulated endogenous NO production in roots and leaves, and on another side SNP treatment also caused the buildup of H_2O_2 in roots and leaves. Chen et al. (2015) studied the

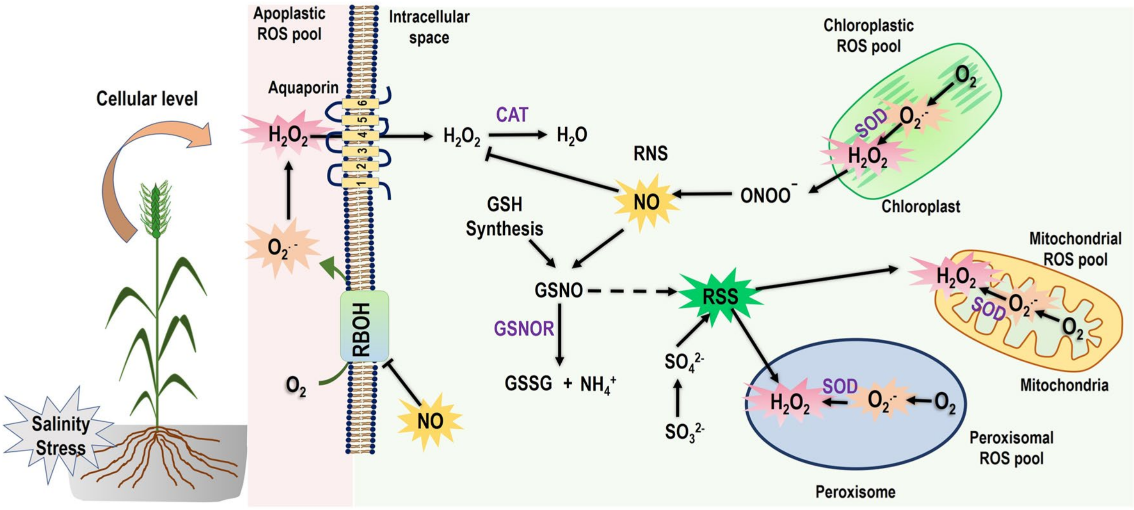

Fig. 2 Conceptual illustration of interaction/interplay between ROS, RNS and RSS in the plant cell under salinity stress condition. ROS ($O_2^{\cdot -}$, H_2O_2) is synthesized mainly in the four pools which include apoplastic, chloroplastic, mitochondrial and peroxisomal pools under salinity conditions. The ROS synthesis also regulates the level of RNS (mainly NO) in the cell which regulates the signalling mechanism. The salinity-mediated synthesis of H_2O_2 by NADPH oxidase enhanced the production of NO which prevent the further accumulation of excess ROS in the cell. The ROS synthesis under salinity stress also enhances the production of RSS (H_2S or GSH). NO react with GSH to form GSNO which is further reduced by GSNO reductase into oxidized glutathione (GSSG). Higher NO accumulation in the cell leads to inhibition of GSNOR and thereby preventing GSNO degradation in the cell. However, the GSNO interaction with ROS is not deciphered (dotted line). RSS interacts with H_2O_2 in the plant cell and counterbalances the level of RSS and ROS in the cell. CAT, catalase; GSNOR, nitrosoglutathione reductase; GSSG glutathione, oxidized form, H_2O_2 hydrogen peroxide, NO nitric oxide, $O_2^{\cdot -}$ oxygen radical, ONOO− peroxynitrite, *RNS* reactive nitrogen species, *ROS* reactive oxygen species, *RSS* reactive sulphur species, *SO* sulphite oxidase, SO_4^{2-} sulphate, *SOD* superoxide dismutase (Color figure online)

interplay between H_2S and NO under salinity-induced barley seedlings and observed enhanced endogenous NO production after external application of H_2S. Both NO and H_2S upregulated the expression of *HvHA1*, *HvSOS1*, *HvVNHX2* and *HvVHA*-β genes which resulted in increased protein expression of PM H^+-ATPase and vacuolar Na^+/H^+ antiporter in salt-induced barley seedlings which indicate that H_2S enhanced salt tolerance in barley seedlings via NO regulated ion homeostasis. A similar type of result was obtained by Wang et al. (2011) where hydrogen sulphide enhanced salinity tolerance in alfalfa at the time of seed germination by diminishing oxidative damage which might be due to interaction with nitric oxide. In both the studies use of NO scavenger transposed the hydrogen sulphide effect on barley seedlings and alfalfa, which indicates the effect of H_2S on endogenous NO levels. da-Silva et al. (2018) investigated whether H_2S acts downstream or upstream of NO during mitigation of salinity stress in tomato. They found that H_2S levels increased by 12–18.9% via NO donor whilst H_2S donor enhanced 10% more NO in tomato roots. Along with this NO comes first in the signalling and involved in the induction of those genes that encodes enzymes responsible for H_2S formation cascade, during attenuation of oxidative stress. This indicated that NO acts upstream of H_2S in the mitigation of salinity stress in tomato. Li et al. (2014) in their study with *Arabidopsis thaliana* root in response to salt stress found that H_2S function as upstream signal of H_2O_2 during alleviating the salinity stress. H_2S enhanced the endogenous H_2O_2 level through regulating the activity of G6PDH (glucose-6-phosphate dehydrogenase) and (PM) NADPH oxidase. Apart from this H_2S upregulated the genes expression and the phosphorylation level of PM H^+-ATPase and Na^+/H^+ antiporter protein level. Mostofa et al. (2015) observed that in rice under salinity stress H_2S pretreatment contributed to the reduction of H_2O_2, LOX activity, MDA content, the elevation of CAT and SOD activity, maintaining GSH level resulting in ROS homeostasis. Lai et al. (2014) found that H_2S pretreatment enhanced the enzymatic activity of GR, DHAR and MDHAR and the abundance of Mn/Cu/Zn-SOD and CAT transcripts as well as regulate the AsA-GSH/hGSH pathway under salinity stress in *Medicago sativa*.

Conclusion and Future Thrusts

The generation of different reactive species (RONSS) and phytohormones in plants in response to salinity stress has been well established and studied. Plants use a combination of different signalling pathways to restore cell homeostasis and survival rate to mitigate salt stress. The ROS production and scavenging always occur simultaneously in the cell, tipping the balance between these, will cause rapid change in ROS levels, thereby generating signals. To prevent damage under different salt stress conditions, plants employ a mechanism that can maintain net photosynthesis with limited CO_2 supply, use alternative electron sinks or the antioxidant defences must keep active oxygen under control. RNS signalling can mitigate the injurious effects of salinity by regulating the SOS pathway, MAPK dependent pathway, Ca^{2+} dependent pathway and G-protein dependent pathway in different crops. Nitric oxide and NO-derived molecules can alter target proteins by the phenomenon of post-translational modifications which plays a pivotal role in the modification of RNS signalling pathways. So far, ROS and RNS have received great attention in all reactive species. However, the participation of RSS is also an important area to understand the salinity stress signalling in plants because these molecules also mitigate the salinity stress through the regulation of sulphur metabolism as well as the synthesis of various sulphur metabolites. H_2S was reported to act as a signalling molecule that interacts with NO and H_2O_2 which impart salinity tolerance. During the plant life cycle from germination to maturity, auxin, cytokinin, gibberellin, ethylene and abscisic acid modulates various growth and development processes of plants. The positive and beneficial effect of exogenous application of different phytohormones under salinity stress might play a crucial role as a free radical scavenger and antioxidative mechanism. Application of some novel phytohormones like salicylic acid, Brassinosteroids and strigolactones (SL) in crops under artificial salinity conditions different types of morphological and biochemical changes were observed.

Despite intensive work revealing nitric oxide diverse functions, reactivity, a signalling molecule and nitrosative stress, the NO production pathway in plants is still poorly understood and remains one of the most puzzling topics in the field. Understanding RONSS-hormonal crosstalk at the gene level is essential to elucidate how plants control salinity-mediated redox metabolism under salinity stress. So far RONSS crosstalk with classical phytohormone is well established but their interaction with novel phytohormones is still in the infancy stage. Identification of different NO/H_2S donors and exact dose of phytohormones for external application will help to mitigate salt stress and to understand their crosstalk with each other. Understanding the complex signalling pathway of different reactive species and using advanced biotechnological approaches like gene editing, RNAi might help researchers to develop varieties with enhanced salinity tolerance. Those genes that impart tolerance against salt stress like Na^+ transporters, ROS scavengers, HKTs and NHXs and others could be combined which might have a positive impact on the plant to cope up with stress conditions. Identification of phenotypic traits with limited genetic complexity and strong correlation to salinity tolerance is crucial for the successful discovery of novel candidate genes and allelic variation therein.

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Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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