Ethylene-Nitric Oxide in Salt Tolerance

Subjects: Agriculture, Dairy & Animal Science

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Salt stress significantly contributes to major losses in agricultural productivity worldwide. The sustainable approach for salinity-accrued toxicity has been explored. The use of plant growth regulators/phytohormones, mineral nutrients and other signaling molecules is one of the major approaches for reversing salt-induced toxicity in plants. Application of the signaling molecules such as nitric oxide (NO) and ethylene (ETH) and major mineral nutrient such as nitrogen (N) and sulfur (S) play significant roles in combatting the major consequences of salt stress impacts in plants. However, the literature available on gaseous signaling molecules (NO/ETH) or/and mineral nutrients (N/S) stands alone, and major insights into the role of NO or/and ETH along with N and S in plant-tolerance to salt remained unclear. Thus, this review aimed to (a) briefly overview salt stress and highlight salt-induced toxicity, (b) appraise the literature reporting potential mechanisms underlying the role of gaseous signaling molecules and mineral nutrient in salt stress tolerance, and (c) discuss NO and ETH along with N and S in relation to salt stress tolerance. In addition, significant issues that have still to be investigated in this context have been mentioned.

FORMAT CHANGE

1. Introduction

As one of the most disturbing environmental stresses worldwide, salt stress has been projected to significantly increase due to the climate change [1][2][3]. Excessive salt concentrations were reported in about 7% of the global land, whereas salt has affected almost 20% of the arable land and 33% of the irrigated land in the world [4]. Additionally, by the year 2050, a continued exposure of arid and semi-arid regions to salt stress is predicted to cause about 30–50% losses worldwide [5]; the salt-affected area is estimated to increase to 16.2 million ha [6]. The increasing land area by salt stress urges plant scientists to build up strategies for sustainable crop production.

The excessive salinity in the rhizospheric zones can negatively affect growth and productivity through creating an imbalance in the cytoplasmic ion homeostasis and thereby impacting metabolic dysfunction and other major biochemical and physiological processes [3][7]. Varied reactive oxygen species (ROS) generated at higher level can occur due to salinity stress in plant cells, can act as signaling molecules, and help in mediating numerous key physiological processes [8]. However, overproduced or non-metabolized ROS can be toxic to plants and cause oxidative damage to cellular constituents including macromolecules (DNA, lipid, and proteins), and, eventually, cause cell death [9][10].

Major mineral nutrients not only constitute a significant part of the agricultural system but also are widely known to modulate the synthesis and production of many plant hormones and thereby help in plant-adaptation to stresses including salt stress [2][11]. Nitrogen (N) and sulfur (S), crucial mineral nutrients (macronutrients), are known to exhibit regulatory interactions and regulate plant growth and development [12]. Notably, the synthesis of most amino acids and proteins, nucleic acids, and several other cellular components involves N [13]. In many instances, N-assimilation and cellular ion homeostasis were reported to contribute in plant tolerance to salt stress [14][15]. On the other hand, owing to its occurrence in various S-containing compounds, it serves as a key nutrient known to improve inherent capacity of plant for stress tolerance [15][16]. Interestingly, most plant nutrients are interrelated with several phytohormones, where their synergistic or antagonistic actions contribute in modulation of the physiological/biochemical responses leading to salt tolerance [2].

Nitric oxide (NO) is a gaseous phytohormone and a reactive nitrogen species (RNS). As a free radical gaseous signaling molecule, NO is involved in plant development and nutrient assimilatory processes and also improves plant tolerance to major stresses such as the soil salinity [17][18][19][20]. Ethylene (ETH) is another gaseous phytohormone that influences plant responses to salt stress [21][22]. Various studies have shown the interaction of NO and ETH with N and S under abiotic stress. Studies have reported the interactive effects of NO with N and S [2] and ETH with N and S [10]. N-availability was reported to influence ETH -production and improve salt tolerance in mustard [23], whereas NO was found to enhance the photosynthetic nitrogen use efficiency (PNUE) and photosynthetic sulfur use efficiency (PSUE). Owing to the occurrence of a close link between the assimilation of N or S with salt stress tolerance, the identification and analyses are imperative to enlighten how much N or S assimilation is induced by phytohormones or vice-versa in order to counteract the salt stress-consequences in plants. The understanding of the role of NO and ETH in the regulation of assimilation of N or S may help in highlighting insights into the plant salt tolerance induced by N- or S-assimilation.

Considering the above aspects, this paper: (i) overviews major salt stress-impacts in plants; (ii) appraises literature available on the role and coordination-outcomes of N and S in plant salt tolerance; (iii) presents discussion on the role of NO and ETH, and the significance of crosstalk of ETH and NO with N and S in plant salt tolerance; and (iv) enlightens so far unexplored aspects in the current context.

2. Salt Stress: An Overview

2.1. Salinity Stress Impacts in Plants

2.1.1. Growth and Development

Salinity-impact on the germination has been reported in several crop plants including *Brassica juncea* [10], *Oryza sativa* [24], and *Triticum aestivum* [25]. In salinity (EC 12 dS m^{-1})-exposed *B. juncea* genotypes, a significant correlation existed between tolerance index and shoot length, dry matter and also salt tolerance efficiency [26]. In addition to significant reductions of shoot and root length, the highest NaCl (200 mM) caused the highest decrease in the germination percentage, germination index and speed of germination in *Helianthus annuus* [27]. Salinity (50, 100, and 150 mM NaCl)-exposed *Pistacia vera* exhibited a negative relationship between salinity stress and vegetative growth parameters [28]. A differential impact of salinity on the fresh and dry weights of the shoot system can be controlled by many factors including changes in salinity concentration, type of salt present, or type of plant species [29]. Compared to roots, salinity regimes impact shoots to a greater extent [30]. In another study, 100 mM NaCl-exposed *Medicago sativa* seedlings showed a marked reduction in dry weight of root and shoot (along with reduced nodulation) [31]. The genotypes of *B. juncea* exhibited greater reductions in shoot and root biomass and leaf area under 50 mM NaCl-exposure [32].

2.1.2. Photosynthetic Functions

Abiotic stresses including salinity have been widely shown to severely impact all the phases of photosynthesis, the most fundamental and intricate physiological process in plants [2][22][33]. In fact, the overall status of photosynthesis can be due to stress-induced change in its various components including photosynthetic pigments and photosystems, the electron transport system, and CO_2 reduction pathways.

Chlorophyll (Chl) is among the sensitive indicators of cellular metabolic state [33]. The content of Chl a and Chl b was significantly reduced under salinity in cucumber seedlings [16]. The photosynthetic pigments as Chl a and Chl b, carotenoids and net photosynthesis rate along with stomatal conductance were highly affected by the salt concentration in water melon plants [34]. In another study, 100 mM NaCl-mediated reduction of Chl a, Chl b and carotenoids contents was shown in rice [35]. In salinity-exposed *T. aestivum*, a greater decline in the photosynthetic rate and electron transport rate and saturating photosynthetically active photo flux density was noted [22]. Moreover, there were reductions in the number of photosynthetic pigments such as Chl and carotenoids with the net photosynthesis, stomatal conductance, intercellular CO_2 concentration, and transpiration rate under stress in tomato plants [36].

The photosystem II (PS II) is the prime site affected by any change in electron transport chain activity due to stress such as salinity [37]. Severe reduction in the efficiency of PS II, the electron transport system, and the CO_2 assimilation rate under salinity stress has been reported [22]. Decreased growth was obtained in barley plants due to salt-accrued damaged Chl fluorescence and oxygen evolving complex [38]. It has been observed that growth becomes reduced in plants due to damage of PS II and electron transport rates under stress [39]. In *B. juncea,* the increased concentration of salt significantly impacted net photosynthetic rate, stomatal conductance, intercellular CO_2, quantum yield of PS II, Rubisco activity, and PNUE [10]. The study of Singh et al. [40] showed the response towards variable concentration of salt, which hampered the photosynthetic apparatus and the water splitting efficiency complex. The photosynthetic pigment content and plant growth were greatly reduced under salinity stress in salt-sensitive *Sorghum* plants [41]. Salt stress was also reported to cause reductions in leaf area, pigment content, Hill reaction, $^{14}CO_2$ fixation, morphology of chloroplasts, number of reaction centers, net CO_2 assimilation rate, and Rubisco activity in wheat [42]. Salinity-mediated down regulation of photosynthetic gas exchange rate, water utilization efficiency was reported to lead to reductions in quantum yield of PS II, photochemistry, and photochemical quenching [43]. Hussain et al. [44] showed that salt stress reduced net photosynthetic rate, and intercellular CO_2 concentration in rice.

2.1.3. Oxidative Stress and Antioxidant Metabolism

Salt stress can enhance the peroxidation of macromolecules through oxidative damage of membrane components [45]. However, peroxidation of lipids can be caused even at mild levels of abiotic stress [46]. In NaCl (0.5, 0.1 and 4 M)-exposed *Dunaliella salina* and *Dunaliella tertiolecta*, increased H_2O_2 content was positively correlated with the level of thiobarbituric acid reactive substances (TBARS) [47]. In *B. juncea*, an increase in TBARS content with increasing the degree of soil salinity was noted by Fatma et al. [16] and Jahan et al. [10].

The major components of antioxidant defense system can be differentially modulated by salinity stress [2][22]. Salinity stress was observed to induce oxidative damage by increasing electrolyte leakage and the contents of H_2O_2, malondialdehyde (MDA), and the activity of superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT) [48]. Salinity-accrued enhancements in the activity of ascorbate peroxidase (APX), CAT, some peroxiredoxins, glutathione/thioredoxin peroxidases, and glutathione S-transferase (GSTs) during salinity stress were argued to be involved in the metabolism of H_2O_2 [49]. In *Glycine max.*, NaCl stress elevated the activity of CAT and APX to minimize the toxic effects of salinity [50]. Salinity-induced increases in the cellular H_2O_2 and concomitant enhancements in the activity of CAT and APX were found in plants [16]. Increased GSH content and elevation in the activity of SOD, H_2O_2-metabolizing (APX), and GSH-regenerating (GR) enzymes were found to be significantly higher in leaves of salt-exposed wheat [22].

2.1.4. Nutrients Uptake, Assimilation and Related Traits

Elevation in the soil salinity impacts the uptake and metabolism of the major plant nutrients including calcium (Ca), potassium (K), phosphorous (P), N and S [10][51]. Changes in K^+-selective ion channels activity or the changes in osmotic potential of solution are bound to reduce the mass flow of most of these mineral nutrients in roots under salt stress [52]. In fact, insufficient supply of one nutrient may affect the amount of the other element which in turn, may hamper the growth of plants by altering their metabolic pathways. Hence, due to the accomplished various roles of these nutrients in plants, they tend to take up (and assimilate) these elements in order to cope particularly with the stressed condition [10]. However, salinity may inhibit or promote nutrient uptake and metabolism by different plant species contingent to types of plants and their organs, salinity levels and nutrients. Salinity stress is known to impact N assimilation by impairing N-uptake, NO_3^- reduction, and NH_4^+ assimilation [53]. In addition, the supply of S to salt-treated plants improved plant salt tolerance [54]. Salinity is known to inhibit K^+ uptake which decreases the K^+/Na^+ ratio and control overall plant salt-tolerance [55]. In fact, salt stress provokes the rapid depolarization of the plasma membrane potential that in turn activates voltage gated GORK (guard cell outward rectifying K^+) channels and results in K^+ efflux [56]. Adverse effects of salinity on PSII activity and eventual hampered growth and productivity may also involve salinity-caused reduced uptake and deficiency of Mn [57]. The solubility and P uptake in plants can also be impacted by changes in soil-Na^+ concentration and pH [58][59].

2.1.5. Crop Yield

The final yield of most crops displayed brutal yield losses even under moderate salt stress may involve changes in the soluble salts in the rhizosphere [60]. Negative association of different yield components with soil-salinity levels has been widely reported [61][62]. Thus, as the main research priority, devising explicit means is imperative in order to recover crop productivity on salt-affected soils (**Figure 1**). To this end, crop breeding comprising both predictable breeding and modern molecular marker-assisted breeding could be of great help [63].

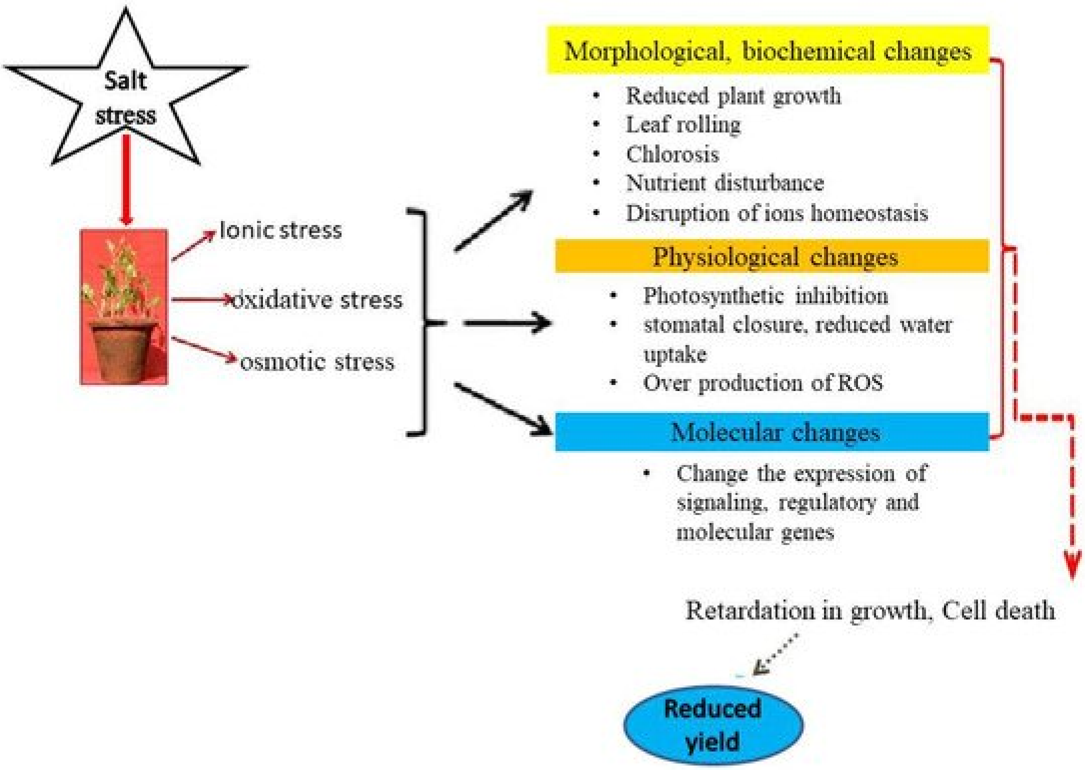

Figure 1. Schematic representation of the major influence of salt stress on plant metabolism and functions.

3. Nitrogen in Salt Tolerance

The uptake of N and its assimilation in plants have been widely found to be impacted by salinity stress [2][64]. Salinity (50 mM NaCl)-mediated decreases in the contents of both N and S were reported in *B. juncea* [65]. In *Hordeum vulgare*, S assimilation was highly impacted with 100 mM NaCl that in turn reduced the cellular thiols (-SH) in plants [66]. The concentration of NaCl (100 mM)-mediated decrease in N uptake was found in *T. aestivum* [64]. There was a drastic reduction of N content in the form of nitrate NO_3^- in the cultivars of *O. sativa* when exposed to 150 mM NaCl [67]. In addition to impacting the content of the major non-enzymatic antioxidants, salt stress inhibited the activity of antioxidant enzymes and enzymes involved in N-assimilation [3][68]. Major genes involved in the uptake and transport of N, and assimilation can also be affected by high salinity [69]. To this end, five genes (*BjAMT1.2*, *BjAMT2*, *BjGS1.1*, *BjGDH1*, and *BjASN2*) were down-regulated, whereas three genes (*BjNRT1.1*, *BjNRT1.5*, and *BjGDH2*) were up-regulated under salt stress [69]. It was concluded that the reduction in NR in plants may lead to down-regulation of gene participating in N assimilation under salinity stress. N-supplementation restricted Na^+-accumulation and improved plant-K status, and thereby increased growth [70]. Furthermore, N-supply also regulated ROS-homeostasis and alleviated salt-toxicity [71]. NH_4^+ supplementation induced salt-tolerance through efficient N-uptake and assimilation processes and controlled K^+/Na^+ homeostasis [72]. The N-supplementation with brassinosteroids seed priming also improved plant salt-tolerance [73].

4. Sulfur in Salt Tolerance

The maintenance of the S-status and the major biochemical and molecular studies to this end have reported to improve plant abiotic stress tolerance [74][75]. In fact, S-containing compounds (including cysteine, Cys; glutathione, GSH) significantly help in cellular redox homeostasis and thereby minimize plant protection against oxidative stress [76][77][78][79][80][81]. GSH acts as an important water-soluble and low molecular weight antioxidant; a major component of AsA-GSH cycle; and the main non-protein source of S to the plants [77][79]. Furthermore, GSH interacts with diverse stress and defense-related signaling molecules and can modulate their pathways, thereby combatting stress-impacts [78]. Adequate S-supply can enhance the content of GSH and improve photosynthetic and growth characteristics in salt stressed plants [16][76]. The imposition of salt stress significantly increased S-assimilation and the biosynthesis of Cys and GSH [2]. In addition, S-supplementation was also observed to improve ascorbic acid (AsA), total phenolics, tocopherol, lycopene, and antioxidant capacity, and decreased H_2O_2 and MDA content in *Z. mays* under salt conditions [82]. S-supply can also attenuate the inhibitory effects of salt stress on gas exchange attributes and growth of lettuce plants, decrease Na^+/K^+ ratio, and improve uptake of K and P [83]. Moreover, supplementation of S reduced the electrolyte leakage and Na^+ accumulation while increasing K^+ and Ca^{2+} and photosynthetic rate under high salt-stressed sunflower plants [84].

5. Coordination of N and S in Salt Stress Tolerance

The major outcomes of the coordinated actions between N and S have emerged as an important strategy for improving plant growth and productivity under environmental stresses [10][65]. In fact, there occurs functional convergence and good coordination between N and S uptake, reduction assimilatory pathways [2][85][86]. The status of nitrate reductase (NR; involved in N-assimilation) and ATP-sulfurylase (ATP-S; involved in S-assimilation) showed mutual interaction in terms of their coordinated role in Cys-synthesis and GSH-production [2]. Particularly, there exists a close relation among GSH and S and N [2]. The availability of its constituent amino acids, Cys, glutamine and glycine are connected with the biosynthesis of GSH which contains three moles of N per mole of S. Notably, the glutamine synthetase (GS)-glutamate synthase (GOGAT) pathway of N assimilation yields glutamic acid; whereas, S-assimilation ends with Cys synthesis [2]. In this way, the coordinative functions of S and N may strengthen plant capacity for stress-tolerance. The literature is full on the recognition of regulatory interactions between N and S assimilation, and its significance in plant stress tolerance [2][65][87]. The synergistic relationship of N and S also contributed in enhancing plant growth, photosynthetic efficiency and proline accumulation under salt stress [88]. The basal supplementation of S with foliarly applied salicylic acid (SA) to salt treated plants modulated enzymes involved in N assimilation, and GOGAT cycle [15]. During N-deficiency, hydrogen sulfide (H_2S) and rhizobia synergistically regulated assimilation and remobilization of N and also modulated senescence-associated genes expression [89]. However, the literature is scanty on N-S interactive effects in minimization of salt toxicity. The synergistic relationship of N and S also contributed to enhancement of growth and crop productivity [87]. The relationship of N and S in terms of crop yield and quality has also been recognized in several studies [87]. It is imperative to unveil more insights into N-S coordination, and their cumulative role in plant salt-tolerance at physiological/biochemical and molecular levels.

6. Nitric Oxide

Nitric oxide (NO), the smallest diatomic gas (30.006 g mol^{-1}), has emerged as a gaseous signaling molecule in plants and has also been reported to exhibit its connection with a range of phenomena from germination and senescence to photosynthesis and cellular redox balance [1][17][79][90][91][92]. NO can easily diffuse across the plant cells and contribute to signal transduction pathways by interacting with different cellular compounds and radicals [93]. Even low (µM and nM) levels of NO can confer plant tolerance to a range of stresses including metal toxicity, salt, drought, high temperatures by mainly modulating the major components of antioxidant defense system and thereby limiting elevated ROS-accrued oxidative stress [1][2][10][17][19][94][95]. Both exogenous supplementation of NO-donors [e.g., sodium nitroprusside (SNP)], NO-scavengers [e.g., 2-(4-carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxyl-3-oxide (cPTIO)] and enzyme inhibitors were widely used to elucidate NO-roles in stressed plants. NO can activate secondary messengers and/or induce transcription of genes and thereby control diverse processes in plants [96]. Moreover, NO can also directly modify proteins, and react with residues of Cys (S-nitrosylation), tyrosine (nitration), or iron and zinc in metalloproteins (metal nitrosylation) [97].

6.1. NO Generation and Signaling

Cytoplasm, chloroplasts, mitochondria and peroxisomes are the major sites of NO-generation in plants [98]. Notably, major pathways for NO generation discovered to date in plants can be categorized into namely enzymatic and non-enzymatic pathways [20]. In enzymatic pathways, cytosolic nitrate reductase (NR; EC 1.6.6.1) and NO synthase (NOS; EC 1.14.13.39) catalyze NO-generation. However, nitrite NO-reductase (Ni:NOR) and xanthine oxido-reductase (XOR) [98][99], and the heme proteins [100] have also been argued to be involved in the enzymatic generation of NO [100]. Moreover, enzyme NO synthase NOS (EC 1.14.13.39) is involved in the production of endogenous NO in mammals [101]. In *A. thaliana* genome, *AtNOA1 (NITRIC OXIDE ASSOCIATED 1*) is indirectly involved in NO production [92].

In plants, enzymatic endogenous NO-generation has been assumed to mainly involve NR [102][103]. Restricted to the cytosol NR has been suggested to catalyze the reduction of NO_3^- to NO_2^- using NADPH as the main electron donor [101]. Nevertheless, revealed through in vitro and in vivo experiments, low oxygen concentration and cellular pH were argued as two of the most important requirements for the activity of NR [102]. In *Arabidopsis*, the NR enzyme encoded redundantly by *NIA1* and *NIA2* genes is capable of reducing nitrite to NO [104]. In addition to highlighted enzymatic sources of NO-generation in plants, NO can be generated non-enzymatically as a by-product of denitrification, fixation of N and respiration. At pH range between 3.0–6.0, AsA-mediated reduction of nitrite yields NO and dehydroascorbic acid [103].

Owing to its lipophilic and highly diffusible in nature, NO is involved in several signaling processes in plants [105]. The list of NO-derivatives, usually referred to as RNS includes NO radicals (NO^-), nitrosonium cation (NO^+), peroxynitrite ($ONOO^-$), S-nitrosothiols (SNOs), higher oxides of N (NOx) and dinitrosyl-iron complexes [106]. S-nitrosoglutathione (GSNO) is yielded as a result of the reaction of NO with reduced GSH in presence of O_2. In turn, NADH-dependent S-nitrosoglutathione reductase (GSNOR) decomposes GSNO to GSSG and NH_3 [107]. NO synthesized during these processes can induce diverse effects in plants [108]. Conflicting reports are accessible about NO induced changes, where some studies show NO as a stress inducing agent [109], even as others have mentioned it as a protective agent [17]. In order to play signaling function, NO has been shown to interact with second messenger, such as, cyclic guanosine monophosphate (cGMP), cytosolic Ca^{2+} ion concentration, and cADP-ribose, phosphatidic acid and ROS [110]. NO-mediated regulation of the activity of enzymes may involve post-translational modifications and joining themselves with metal centers of proteins. NO may also alter the aggregation state, activity, or location of residue of Cys and tyrosine of proteins [97]. NO-mediated nitration of fatty acids is an imperative part of NO signaling in plants [111]. NO can also initiate mitogen-activated protein kinase (MAPK) signaling pathways in plant cells [112]. MAPK cascade (MEK2-SIPK) induces *NO ASSOCIATED1* and NR-mediated NO burst [113]. In particular, SIPK can give positive feedback between NO and ROS signals and MAPK cascades can act to regulate ROS and NO production in plants [113]. Reduction in ROS levels, mitigation of oxidative stress and the role as an anti-senescence agent can be performed by the mitochondrial NOS (*NOS1*).

6.2. Nitric Oxide in Salt Tolerance

The literature supports the involvement of NO in plant stress-response mechanisms, which are largely contradictory, and are contingent to plant species types and the extent of the salt treatment. On the one hand, NO-mediated improvement in plant health was reported to involve improved osmolytes accumulation and strengthened antioxidative defense systems [114]. NO can also mitigate H^+-ATPase inhibition, enhance mineral absorption and maintain hormone equilibrium; and thereby attenuate growth inhibition [115]. The NO-melatonin interaction regulates the expression of Cu/Zn-SOD and Mn-SOD, eventually maintains oxidative homeostasis in plants under salt stress [116]. Moreover, the family of protein kinase is also involved in NO-mediated signaling cascades in salt stressed plants. Furthermore, comparative study of NO and SA was done to study their impact on salt-stress mitigation. The results speculated that NO enhanced salt tolerance due to antioxidant enzymes and compatible solute. However, SA was effective to reduce MDA and H_2O_2 content [117]. The supplementation of NO and jasmonic acid (JA) was reported to mitigate salt stress toxicity through modulation of antioxidant enzymes [94]. NO-interaction with phytohormones can be useful in plant salinity tolerance. In *Arabidopsis*, abiotic stress can reduce root meristem growth by decreasing accumulation of auxin-mediated by NO [118]. The auxin-mediated initiation of NADPH-dependent thioredoxin reductase (NTR) activity is reduced by NO scavengers, signifies that NO is downstream of auxin in this regulatory pathway. NO was observed to efficiently reduce the inhibitory effects of salt stress on growth rates and exosmosis of electrolytes and decreases the lipid peroxidation in wheat as a result of increment in cytokinin (CK) [119]. Furthermore, the supply of absicsic acid (ABA) improves the production and participation of NO downstream of ABA and thereby controls processes including seed germination, dormancy and stomatal movement [120].

7. Ethylene

First identified as a simple gaseous molecule (28.054 g mol^{-1}) ethylene (ETH; CH_2=CH_2), is produced in all higher plants and usually connected with fruit ripening and the triple response. ETH has been reported first as the active component in illuminating gas caused a triple response in etiolated pea seedlings [121]. The development of *A. thaliana* as a model system and eventual development and screening of genetic mutants largely contributed in ETH signaling [122]. The extension in our understanding on how this phytohormone works was possible as a result of the identification of gene array and transcriptional factors working downstream [123].

Ethylene regulates diverse aspects of plant growth responses and development [124] and also plays very important roles in photosynthesis under abiotic stress [22] by regulation of stomatal movement and more influx of CO_2 important for carboxylation [125]. The list of major factors involved in the potential control of ETH-production includes internal signals throughout the development and plant responses under varied abiotic (nutritional disorders, wounding, hypoxia, ozone, chilling, or freezing) and biotic (e.g., pathogen attack) stresses [126]. Furthermore, ETH can regulate H^+-ATPase gene expression and thereby control ion homeostasis in salt stressed plants [127].

7.1. Ethylene Biosynthesis and Signaling

The ETH biosynthetic pathway in higher plants is well described [128][129][130][131]. ETH-production is strictly regulated at various levels and involves both transcriptional [132], post-translational regulation [133]. ETH-signaling cascade starts with first perceived by a family of membrane-bound receptors, predominantly localized at the endoplasmic reticulum (ER). In *Arabidopsis*, ETH-receptors (*ETHYLENE RECEPTOR1* and *2* (ETR1/2), *ETHYLENE RESPONSE SENSOR 1* and *2* (ERS1/2) and *ETHYLENE INSENSITIVE 4* (EIN4) perceive ETH and also involves a number processes [134]. In particular, EIN3 and its close homolog, *ETHYLENE INSENSITIVE3-LIKE1* (EIL1) are key transcription factors activated by EIN2 [135].

7.2. Ethylene in Salt Tolerance

ETH signaling contributes in plant stress responses and tolerance to abiotic stresses including salinity [16][22][136]. ETH can maintain the homeostasis of ions and also up-regulate antioxidant enzymes in plants under environmental fluctuation [137]. Exogenous application of ACC lowered osmotic stress and controlled non-photochemical quenching (NPQ) via PSI cyclic electron flow and starch metabolism in tomatoes under salt stress [21]. MAPK cascade-mediated control of the activation of different defense mechanisms also contributes in response to ROS stress [138].

The supply of ETH-releasing compounds (such as ethephon), ETH-precursors (such as ACC) and/or endogenous ETH-overproduction were reported to confer plant salt tolerance [139][140]. ETH may act as both a positive regulator and or a negative regulator in salt stress-resistance in plants. To this end, application of 1-MCP, an ETH-action inhibitor improved physiological and biochemical antioxidant characteristics [44]. Calcium carbide (CaC_2), a precursor of ETH was reported to exhibit its ability to alleviate salt stress and improve ETH-concentration, seed germination, osmolytes and activities of α-amylase and decrease H_2O_2 and MDA contents under salt stress [141]. Ethylene contribution to salt acclimation processes can differ with respect to the type of response, including improved expression of ETH receptors and ETH production [142]. However, ETH involvement in plant response to salt resistance is highly complex and still remains unclear. In addition, EIN3/EILs are the key elements and positive factors in ETH-mediated downstream transcriptional cascade [143]. EIN3/EILs are involved in many physiological processes, seed germination, apical hook formation, fruit development, abiotic stress and hormone responses [143][144]. A recent report indicates that EIN3/EIL1 are necessary for the enhanced ETH-induced salt tolerance in *Arabidopsis* and salt stress leads to a large number of EIN3/EIL1-regulated genes via promoting EBF1/EBF2 proteasomal degradation in EIN2-dependent and EIN2-independent pathways [145]. Overexpression of EIN3 target genes (e.g., ERFs and *SALT INDUCED EIN3/EIL1-DEPENDENT1* (SIED1)) in a range of plant species leads to salt tolerance [142]. Moreover, melatonin was also reported to enhance plant salt-tolerance by promoting *MYB108A*-mediated ETH biosynthesis [146].

Signaling molecules such as ABA, CK, indole acetic acid (IAA), gibberrelins (GA), ROS, and Ca^{2+} interacts with ETH and thereby contribute in plant stress-adaptation [15][136][147][148]. The DELLA proteins and GA-opposable growth inhibitors of the GA signaling pathway participate in plant salt-tolerance [149]. In particular, ETH-mediated increase in the accumulation of DELLA proteins reduced the action of GA [136]. ABA was reported to regulate the ETH biosynthesis-associated genes (*AtACS5*, *AtACS7*, *TaACO1*, and *GhERF1*) under salt stress [136]. ETH and JA may act synergistically or antagonistically in response to stressed conditions and mediate via EIN3/EIL1 along with *JAZs-MYC2* [150].

The relationship between ETH and SA are antagonistic, conferring tolerance against environmental fluctuation [151]. The application of SA restricted the ETH production by inhibiting the activity of ACC synthase under salt stress [152]. As a result, the reduction in the synthesis of ETH alleviated the toxicity of salt stress. Nazar et al. [153] suggested that SA treatment constrained the ETH formation by inhibiting the ACC synthase activity under drought stress. Interactive outcomes of ETH, H_2O_2, and brassinosteroids were reported to confer plant-tolerance against salt stress [154].

8. Crosstalk of NO with N and S in Salt Tolerance

The NO generation and assimilation of N are closely connected. Both the amount and also the form of the supplied N (i.e., NO_3^- or/NH_4^+) affect levels of NO in plants [155]. Nitrite (NO_2^-) and arginine are the main substrates for NO synthesis. Plants were reported to optimize the use of nitrite as a main source for NO [156]. NO-regimes were reported to exaggerate the activity NR, a key enzyme in N-metabolism, and a NO-source [157]. NO was also argued to modulate the uptake and distribution systems of N [158]. In addition to its role in N assimilation and uptake, involvement of NO in nitrate-sensing pathway was also reported in plants [159]. The reaction of NO with GSH produces GSNO, a low-molecular-weight S-nitrosothiol (SNO). Notably, more stable than NO, SNO serves as a mobile reservoir of NO. However, GSH content can also regulate plant’s S-status through induced S assimilation and forms GSNO [17][160]. The coordination of NO with S can maintain ionic and redox homeostasis, strengthen the plant antioxidant machinery, and thereby improve photosynthetic performance, growth, and salt tolerance [17]. **Figure 2** summarizes N and S assimilation and how their coordination with NO helps in salt tolerance in plants.

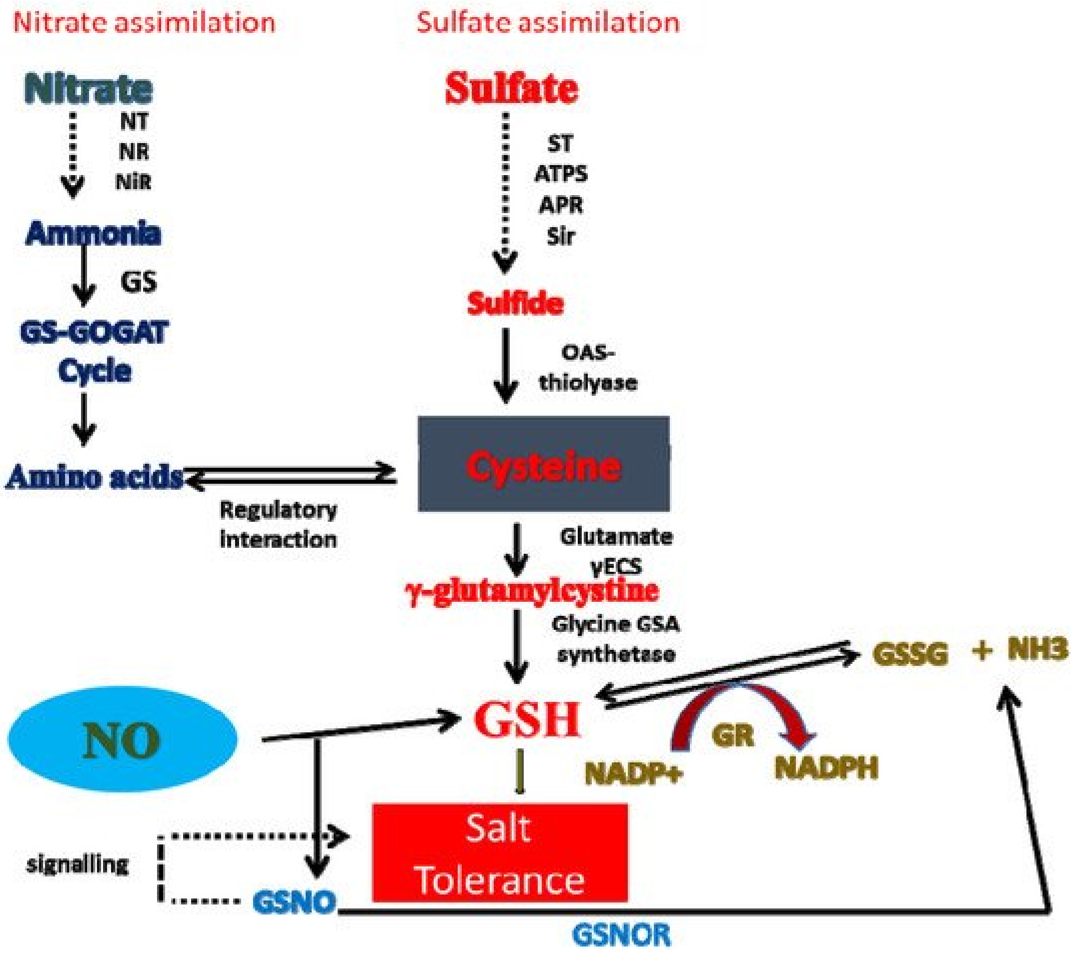

Figure 2. Regulatory interaction between nitrogen (N) and sulfur (S) assimilation and nitric oxide (NO) biosynthesis linked with salinity stress tolerance. APR, adenosine 5′phosphosulfate reductase; ATP-S, ATP sulfurylase; GR, glutathione reductase; GS, glutamine synthetase; GSH, glutathione reduced; GSNO, S-nitrosoglutathione; GSNOR, GSNO reductase; GSSG, glutathione oxidized; NADPH, nicotinamide adenine dinucleotide phosphate;NR, nitrate reductase; NiR, nitrite reductase; NT, nitrate transporter; OAS-TL, O-acetylserine (thiol)lyase; ST, sulfate transporter; SiR, sulfite reductase.

9. Crosstalk of Ethylene with N and S in Salt Tolerance

Interaction-outcomes of ETH with uptake, assimilation of the major mineral elements can contribute in improving plant growth and development under abiotic stresses [10][16]. Deficiency of both N and S is established in the world soils. Hence, maximizing their utilization efficiency in plants is imperative for crop improvement. Studies have enlightened the relation between S-deficiency and ETH-biosynthesis. ETH could ameliorate and regulate S-deficiency in plants [140]. Despite role of N and S in constituting Cys, required for the synthesis of GSH and Met precursor of ETH biosynthesis, the influence of N and S on ETH signaling is meager. As a part of SAM, Met can act as a regulatory molecule in ETH synthesis. The Met pathway is sensitive to salt stress; however, the level of SAM synthase is enhanced significantly under salt stress [9]. In assimilation of N, incorporation of NR into amino acids occurs via GOGAT pathways. Many of these amino acids are involved in ETH-biosynthesis control. Moreover, in addition to increasing N-assimilation, ETH has also been found to regulate proline production in plants under optimum or stress conditions [10][125].

Exogenous ETH through ethephon (ETH releasing compound) can increase N-assimilation and photosynthesis in plants subjected to different levels of N [125]. S-nutrition can modulate plant stress responses by increasing ETH production. Excess S-mediated plant salt tolerance involved ETH, where inhibition of ETH biosynthesis counteracted the effects of S excess on salt stress mitigation [16]. Moreover, the cross-talk between GSH and ETH signaling was proposed under Cd and drought stress [161][162]. However, this is not the only link between ETH synthesis and S. Under S-limited condition, the transcription factor ETH insensitive-like 3 gene regulates many S-deficiency responsive genes [163]. **Figure 3** summarizes the interaction of ETH with N and S.

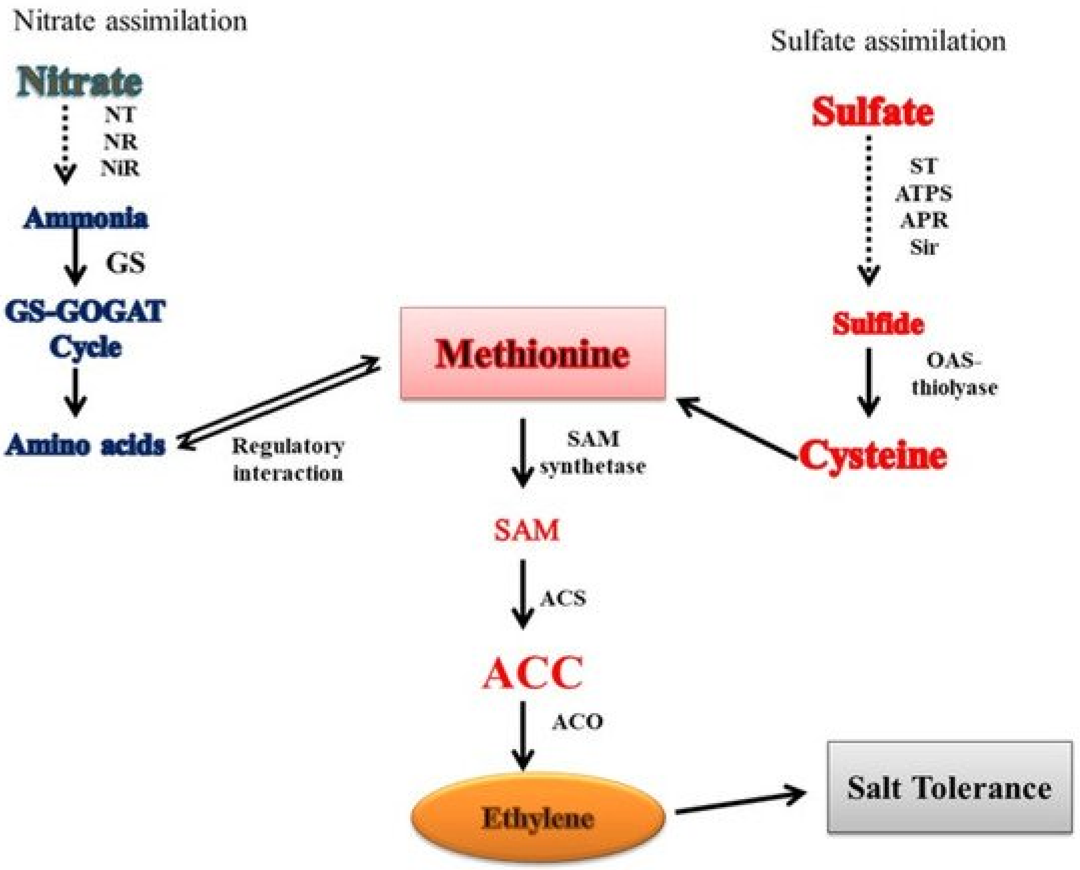

Figure 3. Regulatory interaction between nitrogen (N) and sulfur (S) assimilation and ethylene (ETH) biosynthesis linked with salt stress tolerance. ACC, 1-amino cyclopropane carboxylic acid synthase; ACO, 1-amino cyclopropane carboxylic acid oxidase; APR, adenosine 5′phosphosulfate reductase; ATP-S, ATP sulfurylase; GS, glutamine synthetase; NR, nitrate reductase; NiR, nitrite reductase; NT, nitrate transporter; ST, sulfate transporter; SiR, sulfite reductase; OAS-TL, O-acetylserine (thiol)lyase; SAM, S-adenosyl methionine.

10. Conclusions: Bridging the Gaps in Understanding Salinity Tolerance

The review emphasizes that salt-induced consequences in plants are primarily due to the excess overproduction of ROS resulting in disturbance in plant metabolism and eventually loss of photosynthetic productivity. The appraisal of the studies conducted has shown that plants execute various mechanisms as possible defense strategies to respond the adverse stress conditions. The management of mineral nutrients N or S-mediated regulation serves as a major determinant for depicting salt stress tolerance. Assimilation of N or S leads to the synthesis of Cys that serves as a precursor for the synthesis of a tripeptide GSH which plays a key role in the protection of plants against salt stress. Additionally, the supplementation of N and S and exogenously applied phytohormones prove beneficial for the physiology and metabolism of plants under salt stress, by regulating various metabolic processes as a function of antioxidative defense enzymes. Antioxidants defense system has a constructive function in controlling salt stress in scavenging ROS. Enhanced level of antioxidants enzymes in plants may provide a shield against salt stress through molecular approaches. The literature discussed provides insight on the effects of phytohormones signaling on the regulation of N and S assimilation, GSH synthesis, physiological processes, and productivity of crop species under abiotic stress in general and salt stress in picky. Moreover, diverse studies illustrate the involvement of NO and ETH in providing protection against various environmental stresses, only meager studies discuss the interaction of NO and ETH with N and S with respect to the salt stress. This review also presented a critical crosstalk on NO/ETH, assimilation of N and S, and salt stress (**Figure 4**).

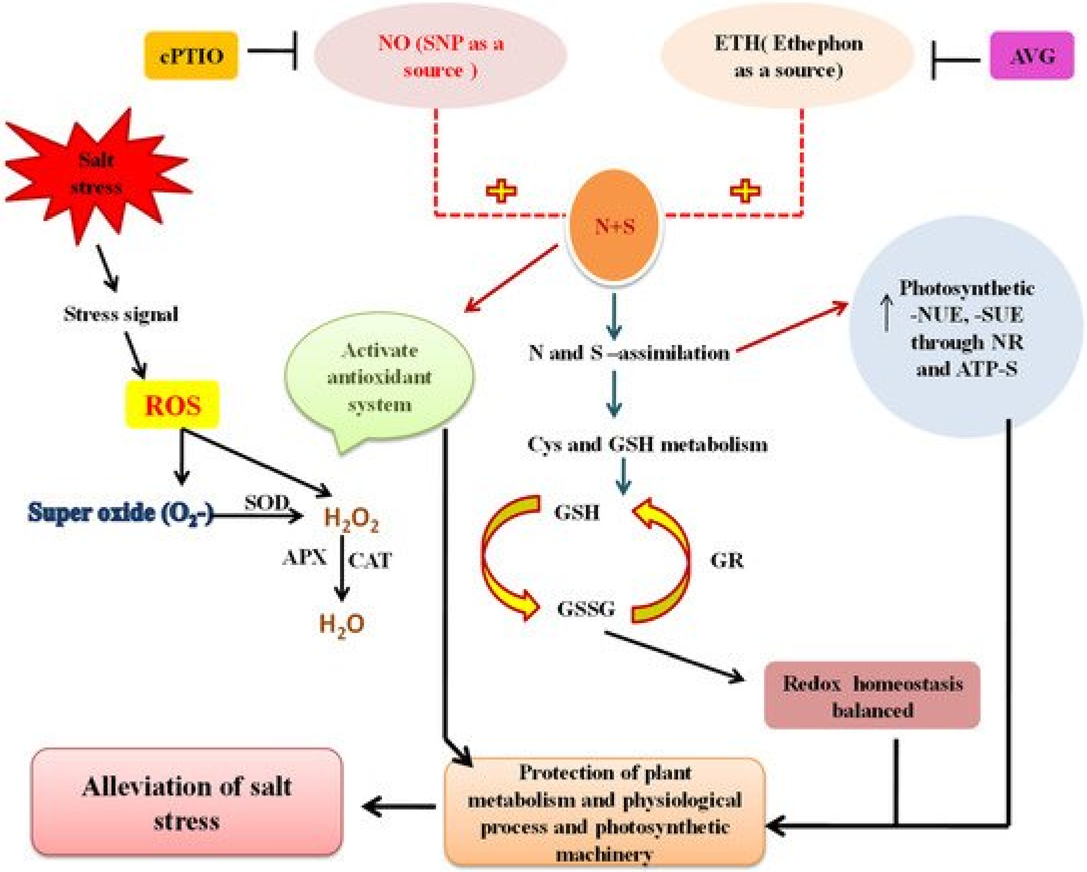

Figure 4. Summary of the major outcomes. The involvement of NO/ETH with supplementation of N and S in alleviation toxicity of salt stress. APX, ascorbate peroxidase; AVG, 1-aminoethoxy vinyl glycine; ETH, ethylene; cPTIO, 4-(carboxyphenyl)-4,4,5,5-tetramethylimidazoline-1-oxy-3-oxide; CAT, catalase; Cys, cysteine; GR, glutathione reductase; GSH, reduced glutathione; GSSG, oxidized glutathione; N, nitrogen; NO, nitric oxide; NUE, nitrogen use efficiency; S, sulfur; SOD, superoxide dismutase; SUE, sulfur use efficiency.

The synergistic relationship of N and S plus phytohormone (ETH/NO) could control plant metabolism and crop yields under salt stress. The interaction between NO/ETH, and N- and S-assimilation, and their assimilatory products makes this approach novel. Thus, the study of the interaction between NO/ETH and N and S is essential as efficient utilization of these nutrients under the influence of these phytohormones will not only benefit photosynthetic and yield potential of plants, but also will result in salt tolerance through the higher synthesis of metabolites. Additionally, the loss of nutrients will be reduced, thereby saving our expenditure on the production of these fertilizers.

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